Phenology, canopy development, biomass and grain yield of annual canarygrass (*Phalaris canariensis* L.)

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Abstract

Canaryseed (*Phalaris canariensis* L.) suffers from low and unstable grain yield. This study investigated whether canaryseed phenological responses to air temperature were associated with grain yield instability.

Two glabrous- and one pubescent-hulled canaryseed cultivars were compared with a cultivar each of a spring wheat with minimum vernalization requirement and an oat cultivar sown at different dates (SDs). Young seedlings were then exposed to vernalizing treatments of 5, 10 and 15°C for 0, 2, 7, 14 and 21 days in controlled-environment experiments.

Canaryseed cultivars generally increased their main stem final leaf number (FLN) with later SDs and reduced their FLN and their leaf stage at floral initiation ($MHLS_{FI}$) upon exposure of the seedlings for up to 14 days at 5°C and 10°C but not at 15°C vernalizing treatments. Both wheat and oat had similar or slightly altered FLN and $MHLS_{FI}$ with different SDs and vernalizing treatments. A putative low-temperature vernalization requirement of canaryseed was therefore proposed.

In the field, FLN of canaryseed was positively associated with the key phenological stages of floral initiation, terminal spikelet formation and anthesis. The length of the pre-anthesis phases with later SDs was altered differentially among canaryseed cultivars but only slightly in wheat and oat. The start of stem elongation in canaryseed was positively associated with FLN, it was negatively correlated with tillering cessation and its duration was shortened with late SDs. In wheat and oat, the start of stem elongation was relatively less affected by SD and tillering cessation was more related to the % of intercepted radiation by the canopy. In canaryseed, earlier tillering cessation together with the suppression of the first few primary tillers may determine tiller number. In wheat and oat, instead, primary tillers were relatively less suppressed. Canaryseed main stem grain yield was relatively stable but tiller-derived yield was positively associated with total plant yield. In contrast, the yield of wheat and oat plants mostly depended more on main stem-derived yield.

The crop biomass, biomass components and grain yield of all five cultivars varied. Canaryseed grain yield variation was best explained by changes in the harvest index. Likely, the canaryseed delayed phenological development negatively affected harvest indices with late seeding. The wheat and oat cultivar, which reached anthesis earlier had lower reductions in harvest index and grain yield.

Canaryseed phenological response to low-temperature can explain part of the grain yield instability.

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Tables of contents

List of Tables

List of Figures

List of Appendices

List of abbreviations and acronyms

Abbreviation	Description
Abbreviations used in the text	
%IPAR	Percentage of Intercepted Photosynthetically Active Radiation
ALL	Actual Leaf Length
ALS	Actual Leaf Stage
CDC	Crop Development Centre
CGR	Crop Growth Rate
CIPAR	Cummulative Intercepted Photosynthetically Active Radiation
DR	Double Ridge
FI	Floral Initiation
FLL	Flag Leaf Ligule
FLN	Final Leaf Number
GLAI	Green Leaf Area Index
GLIMMIX	Generalized Linear Mixed Model
GRAS	Generally Recognized As Safe
HI	Harvest Index
HLS	Haun Leaf Stage
HRS	Hard Red Spring
HS	Haun Stage
IPAR	Intercepted Photosynthetically Active Radiation
k_L	Light extinction/attenuation coefficient
LAI	Leaf Area Index
LSMEANS	Least Square Means
Mbp	Megabase pair
MCPA	2-methyl-4-chlorophenoxyacetic acid
MHLS	Modified Haun Leaf Stage
$MHLS_{2YL}$	Modified Haun Leaf Stage based on the two youngest leaves
$MHLS_{YL}$	Modified Haun Leaf Stage based on the youngest leaf
PAR	Photosynthetically Active Radiation
PPFD	Photosynthetic Photon Flux Density
PTQ	Photothermal Quotient
r^2	Coefficient of determination

RCBD	Randomized Complete Block Design
RGR_{max}	Maximum Relative Growth Rate
RUE	Radiation Use Efficiency
s.d.	Standard deviation
SD	Seeding Date
T	Primary Tiller, followed by numbers denoting the main stem leaf sheath from which a primary tiller appeared
TS	Terminal Spikelet
Tt	Thermal time
ULL	Ultimate Lamina Length

Subscripts

A	Anthesis
E	Emergence
M	Physiological maturity

Abbreviations used in tables and figures only

Adj	Adjusted
AIFR	Average Inflorescence Filling Rate
$AIGR_{TS-An}$	Average Inflorescence Growth Rate from Terminal Spikelet to Anthesis
An	Anthesis
ASER	Average Stem Elongation Rate
BP	Break Point or bilinear or trilinear regression models
df	Degrees of freedom
DM	Dry Matter
F	Estimate (refers to data obtained from FAOSTAT)
FAOSTAT	Food and Agriculture Organization Statistics
Fc	Calculated data (refers to data obtained from FAOSTAT)
FH	Final Harvest
FL	Flag Leaf
IDW_{An}	Inflorescence Dry Weight at Anthesis
IDW_{FH}	Inflorescence Dry weight at Final Harvest
ILA	Individual Leaf Area

Im	FAO data based on imputation methodology (refers to data obtained from FAOSTAT)
$IPAR_{max}$	Beta function estimate of the maximum value of the %IPAR
$MHLS_{YL\_BP}$	$MHLS_{YL}$ at the break point
MS	Main Stem
FPN	Floral Primodia Number
NRCS	Natural Resources Conservation Service
ns, +, *, ** and ***	Symbols used to denote that the level of the statistical significance of mean comparissons is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001
OD	Official Data (refers to data obtained from FAOSTAT)
PAn	Post Anthesis
rMSE	Root Mean Square Error
s.e.	Standard error
SEM	Standard Error of Mean
SH_{max}	Maximum Stem Height
Sign.	Significance
SSE	Start of Stem Elongation
Stat.An.	Statistical Analysis
STT	Secondary and Tertiary Tillers
T_{sec}	Secondary tillers
Tt_e	Beta function estimate of the thermal time after crop emergence when the response variable reached its maximum value
Tt_{Em_An}	Thermal time elapsed from crop emergence to Anthesis
Tt_{IFC}	Thermal time elapsed from crop emergence to Inflorescence Filling Cessation
Tt_{IFD}	Inflorescence Filling Duration in Thermal time
Tt_m	Beta function estimate of the Thermal time after crop emergence when the rate of change of the response variable reached the maximum value
Tt_{SEC}	Thermal time from crop emergence to Stem Elongation Cessation
Tt_{SED}	Stem Elongation Duration in Thermal time
Tt_{TS_An}	Thermal time elapsed from Terminal Spikelet to Anthesis
USDA	United States Department of Agriculture
V.Late	Very Late

Chapter 1 Introduction

1.1 General information on annual canarygrass

Phalaris canariensis L., commonly known as annual canarygrass or canaryseed, is a small-grain temperate cereal, native to southern Europe and the Middle East. Canaryseed is almost entirely used as feed for caged and wild birds (Abdel-Al and Hucl, 2005) usually in mixtures with other grains. The absence of gluten-like proteins in the grain (Boye et al., 2013), novel food approval, and the GRAS (Generally Recognized As Safe) status the seed received in 2016 make it eligible for human consumption and will provide it with the potential to reach the food industry (Canaryseed Development Commission of Saskatchewan, 2018).

Registered canaryseed cultivars in Canada prior to 2001 were pubescent-hulled. The lemma and palea (hulls) enclosing the seed of pubescent canaryseed cultivars are covered by silicified trichomes (hairs) that break off during inflorescence processing (Putnam et al., 1996). These trichomes have been associated with esophageal cancer in humans and skin cancer in animals (O'Neill et al., 1986).

Given these trichome-related issues, the canaryseed breeding program at the University of Saskatchewan has developed glabrous (trichome-free) cultivars (Hucl et al., 2001a). It is the grain derived from these glabrous cultivars that has received GRAS status and could potentially be used for human consumption. Canaryseed is primarily produced in Canada, Thailand and Argentina. It is also produced to a much lesser extent in Hungary, Australia and Uruguay (FAOSTAT, 2018).

The crop has been characterized by yield instability both in Canada (May et al., 2012a) and abroad (Bodega et al., 2003). A 13-fold and 11-fold yield variabilities among site-years have been recorded in rural municipalities across Saskatchewan in 2001 and 2011, due to drought conditions and delayed seeding, respectively (Government of Saskatchewan, 2018a). An even higher variability, approximately 20-fold, has been recorded in experimental field plots (Hucl, personal communication, 2012). The grain yield of canaryseed is approximately half of that of spring wheat (*Triticum aestivum* L.), averaged over the last two decades (Government of Saskatchewan, 2018a).

So far, the response of the crop to agronomic practices, nutrients, fungal and weed control has been researched. Seeding date (SD) has been found to affect seed yield and may account for a fraction of the seed yield variability (May et al., 2012a; Miller, 2000). However, May et al. (2012a) reported that yield reduction due to late seeding alone was inefficient to explain large variations between site years, even when appropriate SDs were used. In field trials

conducted to date, combinations of the factors mentioned above account for less than half of the yield variability among site-years of cultivation.

1.2 Problem statement

Canaryseed production suffers from two major problems: a) grain yield instability among site-years of cultivation (Miller, 2000; Bodega et al., 2003; May et al., 2012a) and b) lower grain yield compared to other small-grain temperate cereals (Miller, 2000). These two problems affect the sustainability of canaryseed grain production. Therefore, research is required to identify potential causes of the relatively low and variable grain yield in annual canarygrass.

1.3 Aim of the research

The aim of the research is to:

1. investigate the causes of the low and variable grain yield of canaryseed and
2. determine means to reduce the large swings in its grain yield.

1.4 Statement of hypotheses

May et al. (2012a) concluded that the environment had a large impact on canaryseed grain yield. However, more research was required to identify potential causes of the relatively low and variable grain yield reported for canaryseed in response to environmental factors.

The following hypotheses have been proposed based on the relatively limited literature on the crop:

1. Canaryseed leaf appearance pattern differs from that of wheat and leaf-development-based phenological scales developed for wheat could underestimate the plant leaf stages.

2. Higher air temperatures with delayed seeding would prevent the fulfilment of a putative vernalization requirement. This would delay key phenological stages, increase the main stem final leaf number (FLN) and delay anthesis. Alternatively, it was hypothesized that increased main stem FLN and delayed anthesis could occur due to the canaryseed leaf appearance pattern.

3. The putative low-temperature vernalization requirement of canaryseed would negatively affect its phenological development, morphology, canopy development, growth, biomass production and grain yield.

1.5 Research objectives

Objective 1 (Chapter 3). To determine the deviation and its magnitude in the comparison of different leaf-development-based scales and to develop an appropriate leaf-development scale for canaryseed.

Objective 2 (Chapter 4). To quantify a potential main stem FLN response of canaryseed to different SDs and relate it to either a potential low-temperature vernalization requirement or to the leaf-development pattern of canaryseed.

Obective 3 (Chapter 5). To investigate the effect of different SDs on main stem leaf phyllochron and to study the tillering pattern of canaryseed relative to spring wheat and oat.

Obective 4 (Chapter 6). To provide information about canaryseed phenological development in relation to different SDs. To assess whether main stem final leaf number response of canaryseed cultivars with different SDs alters main stem morphological characteristics and dry matter accumulation and whether this relates to grain yield. To determine the contribution of main stem- and tiller-derived grain yield in canaryseed. In addition, the development of canaryseed was compared to that of spring wheat and oat, which are both well adapted to local environments.

Objective 5 (Chapter 7). To determine if the reduced grain yield of canaryseed, related to its putative vernalization requirement, is associated with differences in crop biomass production and its components (intercepted radiation and the efficiency with which it is used for dry matter production) or to the dry matter distribution to seed yield (harvest index). Two sub-objectives were addressed: i) to simultaneously compare canaryseed response to environmental conditions with that of two other temperate cereal species with no or minimal vernalization requirements and ii) to investigate genotypic variability for crop biomass production and its distribution to the harvestable product among three canaryseed cultivars.

Chapter 2 Literature review

2.1 Literature review on canaryseed

2.1.1 General information on species origin and taxonomy

Phalaris canariensis L., commonly known as annual canarygrass or canaryseed, is native to the Mediterranean basin and the Middle East. Like other small-grain temperate cereals such as wheat (*Triticum aestivum* L.), barley (*Hordeum vulgare* L.) and oat (*Avena sativa* L.), canaryseed belongs to the botanical family Poaceae and to the subfamily Pooideae. However, it belongs to a different tribe, Agrostideae, than the other mentioned grasses (Putnam et al., 1996). Canaryseed is a predominantly self-fertilizing (Carlson et al., 1996; Matus-Cádiz and Hucl, 2006), diploid species (2n=12) (Matus-Cádiz et al., 2003) with a genome size of 3800 Mbp (Bennett and Smith, 1976). Regarding its carbon-fixation pathway, it is considered a C3 species (Smith and Brown, 1973). Canaryseed is the only annual species of its genus cultivated as a grain crop (Anderson, 1961). An important characteristic of the species is the ripe seed-retaining ability (Oram, 2004 and reference therein), which might have aided its domestication.

2.1.2 Uses of canaryseed grain

Oram (2004) mentioned two references that discuss the use of canaryseed for textiles and as a food grain in the past. Nowadays, canaryseed is almost entirely used as feed for caged and wild birds (Abdel-Al and Hucl, 2005) usually in mixtures with other grains. Over the last decade considerable research has been conducted into new uses and markets for canaryseed. In addition to its potential use in cosmetics and as pig feed (Thacker, 2003), perhaps its most important potential use is for human consumption (Abdel-Aal et al., 2011a; Abdel-Aal et al., 2011b; Li and Beta, 2012).

Canaryseed grain has a potential as an ingredient in carotenoid-enriched functional foods (Li and Beta, 2012). In addition, the absence of gluten-like proteins (Boye et al., 2013), the Health Canada Novel Food approval, and the GRAS status the grain received in 2016 make the grain eligible for human consumption and will provide it with a new market outreach (Canaryseed Development Commission of Saskatchewan, 2018). Two morphological characteristics of canaryseed grain related to its potential for human consumption are described in the following section.

2.1.3 Plant phenology

A study on the morphological variation within and among *Phalaris* species determined that there is limited variation within and among *P. canariensis* accessions in the North American

Phalaris collections (Matus-Cádiz and Hucl, 2002). The main stem height of canaryseed plants at physiological maturity (Figure 2.1) usually ranges from 70 to 110 cm, depending on the cultivar and the environmental conditions; a mean value for each of the 49 accessions of *P. canariensis* reported by Matus-Cádiz and Hucl (2002) under different environments ranged from 70 to 90 cm. Casual observations of canaryseed plants suggest that several tillers usually grow from the main stem leaf axils. Sometimes higher secondary or even tertiary tillers grow (ie, tillers from the leaf axils of parental tillers) and sometimes tillers grow from higher-ranked leaves on the main stems of the plants. Main and tiller stems are thin, usually no more than 2-3 mm in diameter, swollen at the nodes and resistant to bending.

The plant main stem forms several leaves, which, depending on the cultivar and the environmental conditions, can range from less than ten to more than twenty. The length of the main stem leaves may vary depending on the number of leaves and the environmental conditions. The leaf lamina length measured in experiments in the present thesis ranged from 7 to 30 cm. The flag leaf is usually short and thin. That was possibly the reason that Matus-Cádiz and Hucl (2002) reported mean lengths for the penultimate leaves, for comparison purposes, that ranged from 11 to 17 cm.

The inflorescence type of canaryseed is a panicle like oat and rice, but smaller and very compact. Matus-Cádiz and Hucl (2002) reported a mean panicle length of 2.8-3.4 cm and a mean panicle width of 0.8-1.0 cm under greenhouse growing conditions, while those harvested from experimental field plots by the author after physiological maturity showed a range of approximately 1-7 cm in length and approximately 1-3 cm in width. The panicle can contain spikelet numbers ranging from approximately 20 to over 100. The spikelet contains two bract-like and chaffy sterile florets (Matus-Cádiz and Hucl, 2002) at the base of a fertile floret. Canaryseed panicles sometimes show a discoloration and shrinkage of the apical spikelets. These spikelets do not set seed. Such a symptom might be related to environmental stress.

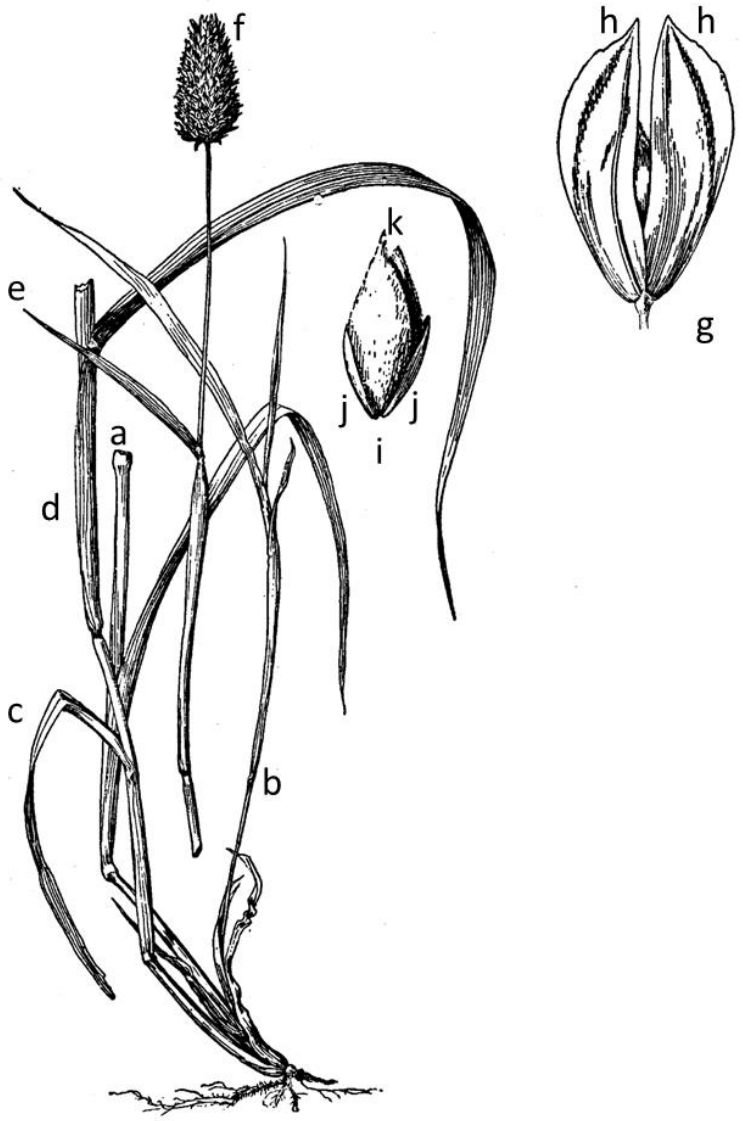

Figure 2.1. Schematic representation of canaryseed main stem (a); tiller (b); leaf lamina (c); leaf sheath (d); flag leaf (e); panicle (f); spikelet (g); glumes (h); spikelet missing outer glumes(i); sterile florets (j); hulls, lemma (left) and palea (right) enclosing caryopsis (k)
Scheme source: USDA-NRCS PLANTS Database / Hitchcock, A.S. (rev. A. Chase). 1950. Manual of the grasses of the United States. USDA Miscellaneous Publication No. 200. Washington, DC.
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Matus-Cádiz and Hucl (2002) reported a mean caryopsis length that ranged from 4.0 to 4.4 mm and caryopsis weights approximately 7-8 mg.

Prior to 2001, registered canaryseed cultivars in Canada were pubescent-hulled. The lemma and palea (hulls) enclosing the seed of pubescent canaryseed cultivars are covered by silicified trichomes (hairs) that break off during inflorescence processing (Putnam et al., 1996). These trichomes have been associated with esophageal cancer in humans and skin cancer in animals (O'Neill et al., 1986). Given these trichomes-related issues, the canaryseed breeding program at the University of Saskatchewan has developed glabrous (trichome-free) cultivars (Hucl et al., 2001a). Canaryseed grain derived from these glabrous cultivars has received GRAS status in the USA and could potentially be introduced for human consumption. Canaryseed grain is typically brown, but the canaryseed breeding program of the University of Saskatchewan has developed a yellow-seeded cultivar. Yellow-seeded cultivars are likely to be prefered for aesthetic reasons over brown-seeded cultivars in products destined for human consumption (Matus-Cádiz et al., 2003).

Canaryseed is a shallow-rooted plant compared to other small-grain temperate cereals such as wheat and oat and therefore may be more sensitive to terminal drought.

2.1.4 Canaryseed as a commodity in Canada and worldwide

Canaryseed is primarily produced in Canada, Thailand and Argentina. It is also produced to a much lesser extent in Hungary, Australia and Uruguay (FAOSTAT, 2018) (Figure 2.2). The average total commodity production worldwide in the chronological periods 2000-2004, 2005-2009 and 2010-2014 was 253, 244 and 215 thousand tons per year, respectively. For comparison, such a production is approximately 0.03% of the corresponding wheat production (FAOSTAT, 2018).

In the last 17 years, Canada produced approximately 72% of the global commodity and 170 Mtons of canaryseed per year (FAOSTAT, 2018). Production of canaryseed in Canada takes place mainly in the province of Saskatchewan (May et al., 2012a), where it is the fourth largest specialty crop. The harvested area for canaryseed in Saskatchewan has ranged from 81,000 to 318,000 ha from 2000 to 2014, representing between 3.4 and 12.7% of the total seeded area for specialty crops (Table 1.1) (Government of Saskatchewan, 2018b).

Thus, while canaryseed is a minor crop worldwide, it is an important commodity for western Canada.

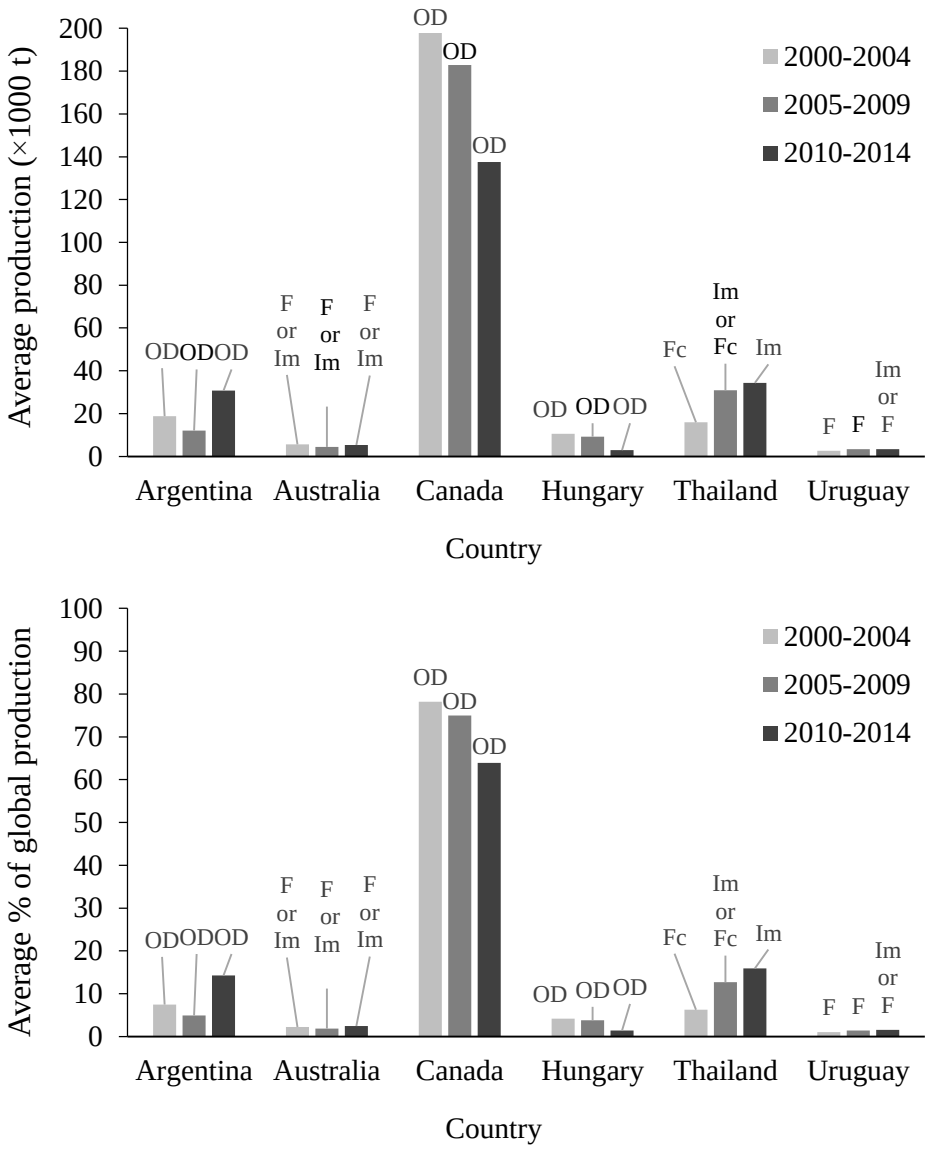

Figure 2.2. Average canaryseed production (top) and average percentage of global production (bottom) for each of the six top producer countries worldwide in the periods 2000-2004, 2005-2009 and 2010-2014 (source: FAOSTAT, 2018).
Abbreviations: Official data (OD); FAO estimate (F); FAO data based on imputation methodology (Im); Calculated data (Fc).

Table 2.1. Harvested area (×1000 ha), grain yield (kg ha^{-1}), production (Mg) and price ($ Mg^{-1}) of canaryseed per year and averaged over five years for the period 2000-2014 in Saskatchewan[1].

	Harvested area[2](×1000 ha)		Grain yield (Kg ha^{-1})		Production (Mg)		Price ($ Mg^{-1})	
Year		Average over 5 years		Average over 5 years		Average over 5 years		Average over 5 years
2000	164		1,035		148,600		259	
2001	163		714		101,200		681	
2002	227		783		142,400		644	
2003	255		877		198,700		379	
2004	318	225	937	869	284,400	175,060	268	446
2005	182		1,232		219,300		201	
2006	131		1,013		129,100		333	
2007	174		927		155,700		525	
2008	162		1,200		184,600		498	
2009	144	159	1,372	1,149	188,700	175,480	402	392
2010	154		998		143,200		546	
2011	109		1,177		128,600		592	
2012	132		1,138		149,700		585	
2013	81		1,468		118,800		495	
2014	107	117	1,165	1,189	124,900	133,040	-	555

[1] Source: Government of Saskatchewan, 2018b.
[2] Harvested area is not necessarily equal to the seeded area

2.1.5 Canaryseed yield-related issues in Canada and abroad

Given that canaryseed achieved GRAS status, new market opportunities would benefit from increased grain production. In addition, an increased net return to the farmers will encourage them to seriously consider canaryseed as an alternative crop option in their rotations.

The crop has been characterized by yield instability in Canada (May et al., 2012a) and in Argentina (Bodega et al., 2003). The main concern of canaryseed growers in an informal survey conducted in Saskatchewan in 1997 was the variation in grain yield among sites and years of cultivation (May et al., 2012a). Similarly, Cogliatti et al. (2011) reported that canaryseed, although adapted to some degree to local Argentinian conditions, still shows marked yield instability over seasons.

Cogliatti et al. (2011) compared 57 accessions of canaryseed in a three-year study in Argentina by means of SDs. They found a 1.8- to 4.1-fold difference in yield for each accession. SDs varied approximately 15 days from year to year.

The grain yield of canaryseed is 44% of that of spring wheat yield, averaged over the last two decades (Government of Saskatchewan, 2018a). Canaryseed harvest index (HI) has been reported between 0.11 (Bodega et al., 1996) and 0.21 (Holt and Hunter, 1987). These values are low compared to spring wheat cultivars (at an average of 0.34) (Wang et al., 2002), to a tall and a semi-dwarf oat cultivar (0.37 and 0.43, respectively) (Rocquigny et al., 2004) or to

Finnish oat cultivars (between 0.45 and 0.49) (Peltonen-Sainio, 2008). Cogliatti et al. (2011) concluded that directing efforts towards increased HI would be beneficial.

So far, the crop response to agronomic practices, nutrients, fungal and weed control has been researched. For example, Holt (1989) and May et al. (2012a) found that increased seeding rates increased yields by 12.5% and by 8.5%, respectively. Weed control did not appear to be a major cause of the observed yield variation (May et al., 2012b). Disease control appears to account for some of the crop seed yield variability (May, 2002). Contrasting information exists in the literature concerning nitrogen effect on seed yield (Holt, 1988; May et al., 2012a). However, experiments conducted across Saskatchewan show that nitrogen does not have a large enough effect to account for the reported yield variability (May et al., 2012a). The application of chloride increased the number of seeds per panicle by 21% as a result of increased panicle size, which caused a 25% increase in the seed yield of annual canarygrass (May et al., 2012b). SD has been found to affect seed yield and may account for a portion of the seed yield variability (May et al., 2012a; Miller, 2000). However, May et al. (2012a) reported that the yield reduction due to late seeding alone was not enough to explain the large variations between site years, even when appropriate seeding dates were used. In field trials conducted to date, combinations of the factors mentioned above account for less than half of the yield variability among site-years of cultivation.

2.2 Literature review on temperate cereals

2.2.1 Introduction

Information regarding canaryseed response to environmental variables is scarce. The current chapter constitutes a review of the literature on the phenology, morphology, biomass, and grain yield of small-grain temperate cereals in relation to temperature, photoperiod, water stress, SD, and crop genotype in the absence of published studies on canaryseed.

2.2.2 Leaf initiation and appearance

Time to anthesis is an important determinant of crop adaptation, especially in temperate environments (Richards, 1991). Rainfed, short-season crop production environments such as those experienced on the Canadian Prairies share characteristics with temperate environments, such as the seasonal variation in temperature and rainfall. The thermal time (Tt) limitation of short-season crop production increases the importance of time to anthesis. Leaf initiation and appearance in cereal crops is a main component of the time to anthesis and therefore, an important characteristic of crop development.

Leaves in cereals, as in all higher plants, are initiated as successive protrusions or primordia due to accelerated cell division and growth by their stem apical meristem (Steeves and Sussex, 1989). Subsequently, leaf primordia expansion takes place from the cell division of the intercalary meristem and growth of cells derived from the intercalary meristem resulting in leaf lamina and sheath appearance (McMaster et al., 2003). Expansion or unfolding of laminae and sheaths continues until all the leaf primordia that are committed to vegetative development appear on plant stems.

The quantitative terms *plastochron* and *phyllochron*, which are the inversed rates of primordium initiation and leaf appearance, respectively (Wilhelm and McMaster, 1995), are generally used to compare plant or crop performance. Leaf primordium initiation and expansion and therefore plastochron, are mainly determined by tissue temperature. Leaf appearance also depends on other factors, such as carbohydrates, nutrients, water availability, and light quality and quantity (McMaster et al., 2003).

Plastochron depends on SD in winter wheat (Baker et al., 1980; Porter et al., 1987), spring wheat and barley (Miralles and Richards, 2000; Miralles et al., 2001), and oat (Sonego, 2000). Plastochron also depends on the genotype vernalization and photoperiod requirements and the degree of their fulfillment as demonstrated in wheat (Hay and Kemp, 1990; Kirby, 1990; Brooking, 1996; Brooking and Jamieson, 2002). For instance, primordium initiation rate, per main stem leaf, is often separated in two distinct phases. The first phase has a lower rate compared to the later one in wheat (Kirby, 1990) and oat (Sonego, 2000). When plants have not fully met their vernalization and/or photoperiod requirements, the difference between the primordium initiation rates in the two phases becomes smaller or even undetectable (Brooking and Jamieson, 2002). Plastochron also depends on genotype in wheat and barley (Frank and Bauer 1995; Miralles et al., 2001) and in forage grasses (Frank and Bauer, 1995). In addition, in barley, water stress causes primordium initiation to cease while floral development at the stem apex continues (Singh et al., 1972).

Phyllochron, in turn, depends on SD for winter wheat (Baker et al., 1980; Porter et al., 1987), bread wheat and barley (Miralles et al., 2001), oat (Sonego, 2000) and triticale (× *Triticosecale* Wittmack) (Giunta et al., 2001). Since different SDs usually involve contrasting air and seedbed temperatures, and/or photoperiods, efforts have been made to relate these environmental factors to changes in phyllochron. Studies have dealt with the hypothesis that temperature *per se* at or near the seedling crown are closely related to the phyllochron in wheat (Jamieson et al., 1995a; McMaster et al., 2003; Jamieson et al., 2008). Indeed, temperature does correlate with phyllochron, but only within temperature regimes depending on factors, such as species and

genotype, while phyllochron levels off at higher temperatures (McMaster, 2005 and references therein). Other studies, however, suggested that differences in the phyllochron among SDs are associated with the photoperiod at crop emergence and the direction and change of the photoperiod for wheat (Baker et al., 1980; Wilhelm and McMaster, 1995) and oat (Sonego, 2000). Even the FLN on plant main stems has been related to phyllochron while later emerged leaves of plants with increased FLN due to vernalization or photoperiod responses exhibited a higher phyllochron compared to earlier emerged leaves (Miralles and Richards, 2000). More recent experiments that deployed plant materials with systematically different vernalization and photoperiod sensitivity in the same background showed interactions between FLN, sensitivity to vernalization, and photoperiod (Steinfort et al., 2017). These experiments showed that, depending on the allelic combination of the near isogenic lines used, not only linear but also bi- or even trilinear models described the phyllochron and its magnitude with Tt, even for treatments resulting in similar FLNs.

Nutrient availability has also been related to phyllochron in barley (Prystupa et al., 2003; Arisnabaretta and Mirrales, 2004) and wheat (Salvagiotti and Mirrales, 2007). Nitrogen fertilization showed inconclusive or not obvious results (Cartelle et al., 2006; Alzueta et al., 2012). Phyllochron becomes shorter due to water stress in triticale (Estrada- Campuzano et al., 2008). However, nutrient or water availability stress affects phyllochron to a lesser extent.

Phyllochron also depends on the genotype of wheat and barley (Frank and Bauer, 1995; Miralles et al., 2001), forage grasses (Frank and Bauer, 1995), oat (Sonego, 2000) and triticale (Giunta et al., 2001; Campuzano-Estrada et al., 2008).

Given that both plastochron and phyllochron are affected by the same factors, phyllochron, which follows plastochron of a particular leaf, is likely affected by the latter. Apart from the factors affecting plastochron and phyllochron, their ratio depends on the species. For instance, the plastochron:phyllochron ratio in winter wheat and barley is about 2:1 (Baker and Gallagher, 1983a; Kiniry et al., 1991) but in oat is about 1.7:1 (Sonego, 2000).

2.2.3 Tillering

A *tiller* is a branch that results from differentiation and upright growth of an axillary bud on the stem of plants in the family of grasses (Poaceae). The tillering pattern of a crop, an important morphological characteristic of cereals, is often studied in relation to main stem leaf appearance because in two major cereal species, wheat and barley, main stem phyllochron is closely associated to tiller appearance (Klepper et al., 1982; Kirby et al., 1985). Therefore, factors

affecting leaf initiation and appearance may potentially affect one or more components of a crop tillering pattern.

Axillary bud growth depends on a number of plant internal (ie, assimilate availability and hormonal signaling) and environmental factors (ie, light signaling and intensity and nutrient availability) (Evers et al., 2011 and references therein). Each tiller has a time window within which the axillary bud may break (Klepper et al., 1982).

The quantitative terms maximum tiller number, time or plant Haun leaf stage at tiller appearance and cessation, tiller appearance rate (number of tillers that appear per unit of time or Tt and per plant or per unit of land area) and duration (period of time or Tt from the onset until the cessation of tiller appearance) are often used to facilitate comparisons in plant or crop performance.

Regarding the effect of photoperiod on tillering, under long days at high latitudes, plant height strongly controls tiller growth, with duration to maturity and/or heading positively correlating to tiller number in wheat, barley, and oat, though at the expense of tiller HI (Peltonen-Sainio et al., 2009).

Different SDs at higher latitudes expose crops to different photoperiods and often different temperature regimes. Vernalization and/or photoperiod responsive genotypes show alterations in their phenological phases, often accompanied by changes in the FLN (eg, Brooking and Jamieson, 2002). Such a response relates to the maximum number of tillers that appear per plant, in controlled-environment studies (Hucl and Baker, 1990) and in the field, for wheat (Miralles and Richards, 2000; Dreccer et al., 2013; Steinfort et al., 2017) and barley (Miralles and Richards, 2000). However, as Dreccer et al. (2013) discussed, different processes may be important for tillering depending on the component trait and the way that it is affected, which depends on the population under study.

In wheat genotypes differing in tillering capacity, Spielmeyer and Richards (2004) and Kuraparthy et al. (2007) described genes that influence bud differentiation and growth, while the agronomic evaluation of the tiller inhibition (*tin*) gene (Spielmeyer and Richards, 2004) shows promising results especially under terminal drought conditions (Duggan et al., 2005b).

Water availability potentially affects the leaf mass per area (Poorter et al., 2009) of individual leaves, and therefore the probability of tiller bud-break as shown in spring wheat (Evers et al., 2006), tillering cessation through changes in the red:far-red ratio within the crop leaf canopy (Evers et al., 2006) and/or its fraction light interception (for wheat: Evers et al., 2006; for barley: Alzueta et al., 2012). Finally, increased tillering in early crop stages and high

canopy ground cover has been related to lower soil moisture loss or higher moisture conservation via lower soil evaporation (Berry et al., 2003; Borras-Gelonch et al., 2010).

2.2.4 Plant phenology: a short description

Early developmental events expressed phenotypically at the plant main stem apex were described in Section 2.2.2 (leaf initiation and appearance). The following information refers to wheat phenology unless otherwise stated. As mentioned earlier, the change in the rate of primordium initiation at the shoot apex takes place once the plant has met its vernalization and/or photoperiod requirements. In the literature, that particular stage is often described as floral initiation (FI), although the fulfillment of plant requirement(s), in terms of vernalization and/or photoperiod, may be met either at or prior to FI (Brown et al., 2013). The primordia that appear after FI may become leaves or spikelets, depending on the rate of the two processes that occur simultaneously but have opposite 'directions'. These two processes are the commitment of leaf primordia to become leaves and the commitment which will overgrow the leaf primordia with spikelet primordia (Griffiths et al., 1985; Brooking and Jamieson, 2002). The spikelet primordia are initiated in the axils of the leaf primordia. An important event that takes place after FI is the appearance of double ridges (DR), defined as the phenological stage at the appearance of spikelet primordia on top of equal-size leaf primordia, near the center of the spike. Besides DR, another important event is the final or terminal spikelet (TS) primordium formation at the top of the shoot/stem apical meristem which indicates the cessation of spikelet initiation. In contrast to wheat, barley does not have a true TS as its inflorescence is indeterminate. The corresponding stage of TS in barley is considered to be the appearance of awn initials because spikelets formed after that stage usually fail to further differentiate and grow (McMaster, 2005). Two differences in the phenology between wheat and oat occur at the FI and TS stages. The FI stage in oat, as expressed phenotypically at the stem apex, is almost identical to the DR stage as shown by Sonego (2000) and the top spikelet is the first one to be formed at the top of the stem apical meristem while the 'direction' of commitment of spikelet primordia initiation moves basipetally (towards the base of the inflorescence) (Sonego et al., 2000). The overgrowth of leaf primordia subtending the spikelet primordia occurs in the leaf primordia located between the DR and the last expanded leaf primordium. Hence, the main stem FLN cannot be identified among the leaf primordia and can only be determined once the plant FLN is known (Jamieson et al., 1998). Once the plant 'has decided' which leaf primordium is the final one to form a leaf, and all initiated leaf primordia above the final leaf primordium are overgrown by spikelet primordia, all leaf primordia will first expand and appear

on the main stem of the plant before rapid stem elongation begins. After the inflorescence swells in the boot, it will subsequently emerge above the flag leaf and reach anthesis and eventually physiological maturity.

Jamieson et al. (2007) demonstrated that the Haun leaf stage (Haun, 1973) at the TS stage is closely related to the FLN as did Sonego et al. (2000) in oat. Based on these findings, Brown et al. (2013) noted that the environmental cues that determine the two opposite 'directions' of commitment, the leaf primordia to become leaves and the spikelet primordia to overgrow the leaf primordia, will eventually determine the plant FLN. Therefore, based on Brown et al. (2013) the time of anthesis in wheat is determined by vernalization and photoperiod effects on the plant FLN and temperature and phyllochron effects on the time it takes for the flag leaf to appear. Other studies, however, in the context of increasing grain yield potential, point to the fact that the period of time between the initiation of TS and heading may be modified by photoperiod at the expense of earlier phases (Slafer, 1996; Miralles et al., 2000; Gonzalez et al., 2011b). Another study by Dyck et al. (2004) showed delayed heading (on average by three days) in spring wheat isolines with the PPD-D1-sensitive allele when sown at higher latitudes across North America. Steinfort et al. (2017) recently published a study on wheat lines differing in vernalization and photoperiod sensitivity in the same genetic background and demonstrated that, although photoperiod sensitivity may affect a phenological phase (ie, stem elongation phase) generally, when a phenological phase was extended, time to anthesis was somewhat or substantially extended.

Temperature and often photoperiod are the two most critical factors determining temperate cereal phenology (Baker and Gallagher, 1983a and b; Cao and Moss, 1989a and b; Sonego, 2000). Information regarding the effect of temperature on aspects such as the plastochron and phyllochron have been reported earlier in this chapter. The effect of temperature during the vernalization process is covered in a following section. The effect of photoperiod on temperate cereal phenology will be reviewed along with the effect of vernalization in a subsequent section of this literature review.

Water availability may affect phenology in wheat (McMaster, 1997; McMaster and Wilhelm, 2003; Estrada-Campuzano et al., 2008), barley (McMaster and Wilhelm, 2003) and triticale (Estrada-Campuzano et al., 2008), while water stress may reduce the phyllochron, likely through reduced leaf growth and expansion (McMaster, 2005), or decrease the duration of developmental phases via increased crop leaf canopy temperature (Estrada-Campuzano et al., 2008). The effect of water availability on the phyllochron appears to be substantially smaller (Baker et al., 1986) relative to that of temperature and photoperiod. However, lower water

availability may reduce the Tt required to complete later crop growth phases, such as grain filling (McMaster and Wilhelm, 2003), without necessarily having negative effects on yield, such as under irrigation with fertilizer application (Yang and Zhang, 2006).

The effect of SD on temperate cereal phenology are mainly covered in the chapter dealing with the effects of temperature and photoperiod. The water availability, as a component of the confounding effects of different SDs, will be covered separately, while other components, such as light intensity and quality that may also change with SD, are beyond the scope of this literature review. Genotypic effects on temperate cereal phenology are related to genotypic effects on plastochron and phyllochron as well as vernalization and photoperiod sensitivity. Therefore, this information is reported in other individual sections of the present review.

2.2.5 Vernalization

Plants adapted to temperate climates usually exhibit a requirement for low-temperature vernalization (the term vernalization will be used hereafter unless otherwise stated). Such a requirement may postpone the onset of floral primordia to coincide with more favorable environmental conditions. In addition to the vernalization requirement, Summerfield et al. (1997) postulated that most crops of Mediterranean or temperate origin, including cereal species (Thomas and Vince-Prue, 1997), are long-day plants. Such a requirement often prevents plants with lower vernalization requirements, relative to the prevailing temperatures, from forming reproductive organs before the photoperiod increases, such as with the more favorable growing conditions of springtime. This is due to the higher vulnerability of floral structures, compared to leaf primordia, to wintertime freezing temperatures as discussed for wheat (Single, 1985), which is crucial for the perpetuation of the species. Plant response to photoperiod is often characterized quantitatively (facultative), when plants accelerate the formation of reproductive organs as day length increases, or qualitatively (obligate) when a plant requires a minimum number of hours *per diem* to start to form reproductive organs. In the following section of this review, the effect of photoperiod during the vernalization process will be reviewed.

2.2.6 When and how do vernalization and photoperiod act?

Temperate cereal responses to vernalization, photoperiod, and their interaction are phenotypically expressed as changes in the FLN produced on the plant main stem (Brooking et al., 1995; Mahfoozi et al., 2001a and b; Brooking and Jamieson, 2002). Vernalization under an inductive photoperiod in spring wheat isogenic lines with vernalization requirements lowers the FLN while under a short photoperiod increases the FLN by causing the appearance of FI and TS at the stem apex to occur at earlier and later plant physiological ages (ie, Haun leaf stage),

respectively (Brooking, 1996; Robertson et al., 1996; Brooking and Jamieson, 2002). The delay of FI and TS appearance depends on the temperature and duration under that photoperiod (delays in both stages occur in the same manner). In addition, in spring wheat isogenic lines, the duration from FI to the TS is approximately two leaf stages under an inductive photoperiod, but under a shorter photoperiod the results are inconclusive (Brown et al., 2013). Therefore, vernalization responses in wheat are confined to phenological phases prior to the FI at the stem apex (Brown et al., 2013).

For a given photoperiod, the physiological age required for a spring isogenic line after its exposure to inductive conditions, to trigger FI and TS is constant, but the chronological time required depends on the temperature (as the Haun leaf stage increases linearly with temperature within a temperature regime) (Brown et al., 2013).

For a winter wheat isogenic line, the vernalization and photoperiod interact to influence the time of FI. A short photoperiod accelerates the appearance of FI relative to the inductive photoperiod (short-day vernalization). In addition, the duration from the FI to TS phases increases in response to the short photoperiod (Brown et al., 2013). A similar response was reported in other temperate cereals such as a Syrian land-race barley accession (Roberts et al., 1988) and in a barley cultivar (Limin et al., 2007).

2.2.7 Biomass production and its components (radiation interception and its use efficiency)

2.2.7.1 Canopy components and radiation interception

i. Seedling leaf characteristics and seedling vigor

Differences in early seedling vigor associated with the characteristics of early seedling leaves exist among temperate cereals. For instance, leaf area and specific leaf area index (= 'leaf mass per area'$^{-1}$ = leaf area:leaf dry mass) in early main stem leaves, which, in turn, was positively associated with embryo seed size, has been reported to confer higher early vigor in barley and to a lesser extent in triticale in comparison to wheat and oat (Lopez-Castaneda et al., 1996). Similarly, higher leaf area of early main stem leaves (Lopez-Castaneda et al. 1995) or higher early green area index and specific leaf area (Sieling et al., 2016) have been reported for barley compared to wheat. Such differences among temperate cereals suggest differences in early crop leaf stages radiation interception.

ii. Main stem vs tiller and higher vs lower FLN with respect to leaf area

Tiller presence influences light interception by the crop leaf canopy, often increasing it due to higher leaf number plant $^{-1}$ and/or m^{-2}. However, the suppression of a number of tillers in

wheat showed no or minimal differences in light interception between lines with or without the tin gene as a result of longer and wider earlier- or later-developed main stem leaves (Duggan et al., 2005a and references therein). Nevertheless, differences in the interception of photosynthetically active radiation (IPAR) at early crop stages, due to differences in leaf area indices, do not necessarily translate into higher leaf area index (LAI) and IPAR around anthesis. Green leaf area and non-senescing tiller maintenance is not guaranteed, as shown in two-row barley (Prado et al., 2017) and wheat lines with vernalization and/or photoperiod sensitivity (Steinfort et al., 2017). In Steinfort et al. (2017), the higher main stem FLN of wheat lines with unmet vernalization requirements did not increase light interception because of their substantially lower area compared to corresponding leaves in vernalized treatments.

iii. Flag leaf area

Kirby et al. (1982) reported differences in flag leaf size in barley cultivars classified as winter types sown on different dates. However, they found no differences in flag leaf size between dates with short photoperiods and low temperatures. Similarly, Steinfort et al. (2017) reported differences in the flag leaf area in wheat lines differing in vernalization and/or photoperiod sensitivity. Flag leaf area of the unvernalized winter types was up to a 43% smaller than that of the vernalized ones. This smaller flag leaf area was accompanied by higher FLN and shorter phyllochron. The inverse was observed from lines growing under a short photoperiod. In contrast, potentially unvernalized field-grown winter wheat genotypes had increased leaf dimensions and were not markedly affected by photoperiod, while smaller higher order main stem leaves were associated with a low N level (Hotsonyame and Hunt, 1998).

iv. Water availability and effects on LAI and IPAR

Water availability likely affects the crop leaf canopy of temperate cereals via individual leaf cell growth and expansion. Muurinen and Peltonen-Sainio (2006) reported low green LAI (GLAI) due to water shortage in wheat, oat, and barley cultivars at high latitudes. Maximum LAI values of rainfed crops seeded at intermediate rates (350 seeds m^{-2}) are reported between approximately 4.0 and 10.0 and from approximately 7.5 to 10.0 in wheat and triticale cultivars, respectively, while the values for irrigated treatments were approximately 12 or higher (Estrada-Campuzano et al., 2012). Therefore, maximum LAI is likely lower in rainfed small grain temperate cereal crops than in irrigated ones.

Maximum LAI values for rainfed spring wheat cultivars in the semiarid Canadian Prairies have been reported between 2.5 and 3.5 (for a seeding rate of 250 seeds m^{-2}), with year of cultivation showing higher differences than the cultivar, while SDs did not have a significant

effect (Hucl, 1994). However, as Hucl (1994) discussed, the fact that cultivars, and not near isogenic lines, were used in the study might masked potential SD effect on LAI. In oat, maximum LAI in the Canadian Prairies has been reported higher than 7.0 (for a seeding rate of 240 seeds m^{-2}) (Ross et al., 2005). In a comparative study between the two species in eastern Canada, LAI values for wheat and oat at anthesis were between 0.5 to 3.0 and 1.3 to 4.7 in nitrogen-fertilized plots and between 0.8 to 2.0 and 1.3 to 2.7 in plots receiving no nitrogen fertilizer (seeding rate of 300 seeds m^{-2}) (Ma et al., 2012). LAI values for rainfed temperate cereal cultivars seeded at high rates (500 to 600 seeds m^{-2}) at high latitude cropping systems were reported from approximately 1.8 to approximately 4.0 for oat, from approximately 1.5 to approximately 5.0 for two-row barley, from approximately 1.5 to approximately 3.5 for six-row barley, and from approximately 1.0 to approximately 2.5 for spring wheat (Muurinen and Peltonen-Sainio, 2006).

Light extinction or attenuation coefficient (k_L) within the crop leaf canopy determines the amount of incident IPAR by the canopy, especially at lower LAI values. k_L values depend on species and cultivar morphological characteristics but are also affected by crop management practices, including water availability, which reduces k_L values by up to 26% in wheat and triticale (Estrada-Campuzano et al., 2012). k_L values for rainfed temperate cereal cultivars seeded at high rates (500 to 600 seeds m^{-2}) and different N application rates at high latitudes ranged from 0.53 to 0.68 for oat, from 0.50 to 0.84 for two-row barley, from 0.58 to 0.91 for six-row barley, and from 0.62 to 0.79 for spring wheat (Muurinen and Peltonen-Sainio, 2006). k_L values reported for barley for a wider range of factors (ie, cultivars, time of sowing, and soil moisture) ranged from 0.39 to 0.66 (Gregory et al., 1992; Goyne et al., 1993) and for wheat in Mediterranean or semiarid environments from 0.38 to 0.82 (Yunusa et al., 1993; Miralles and Slafer, 1997; O'Connell et al., 2004).

None of the studies referenced in Canada reported k_L values. If the critical LAI value of a crop is when its leaf canopy intercepts nearly 95% of the incident PAR and, assuming that k_L values of rainfed temperate cereal crops sown at moderate rates (ie, wheat and triticale seeded at a rate of 350 seeds m^{-2}) and receiving no fertilizer application are near 0.35 (Estrada-Campuzano et al., 2012), critical LAI values of temperate cereals in the Canadian Prairies would be near 8.5. If k_L values were 0.40, 0.45 or 0.50, then the critical LAI would be 7.5, 6.5 and 6.0, respectively. Such critical LAI values are either near or well below the maximum LAI values reported in most cases in the studies referenced, which suggests that rainfed temperate cereal crops in the Canadian Prairies intercept lower PAR levels than the incident ones, even at maximum LAI values.

Maximum LAI values in rainfed temperate cereals are also affected by the timing of potential water stress. For instance, pre-anthesis drought, when crop leaf canopies are formed, affect maximum LAI values more than post-anthesis drought, which lowers the crop IPAR, as shown in wheat (Estrada-Campuzano et al., 2012) and triticale (Giunta and Motzo, 2004; Estrada-Campuzano et al., 2012).

v. Seeding date effect on LAI and IPAR

Different SDs may modify the cycle length and/or the length of individual phenological phases in response to vernalization, photoperiod, or their interaction with corresponding changes in water availability and in the incident and intercepted solar radiation (eg, Steinfort et al., 2017). However, the effect of SD on vernalization and photoperiod insensitive genotypes (providing that water and nutrient availability have relatively smaller effects on phenology) would likely only shift the crop cycle length.

2.2.7.2 Radiation use efficiency (RUE)

The efficiency with which crops use the radiation intercepted by their leaf canopies to produce biomass is a physiological characteristic used in the interpretation of crop response to abiotic environment (eg, temperature, irradiance, water availability), genetic variation, and crop management practices (eg, water and nutrient supply, plant population density, and SDs). Reported RUE values in this section are based on intercepted PAR unless otherwise stated.

i. Water availability

Monteith (1977) concluded, for a range of crops, that stress may affect radiation interception more than the RUE. Subsequent studies on cereals showed that drought reduced RUE predominantly in several triticale cultivars (Estrada-Campuzano et al., 2012), while in certain triticale cultivars and a single wheat cultivar, drought stress reduced IPAR or RUE, depending on the stage of canopy development when the stress was imposed (Estrada-Campuzano et al., 2012). Earlier studies reported similar results for barley and triticale (Fukai, 1995; Jamieson et al., 1995b; Giunta and Motzo, 2004). Temperate cereal crops with lower k_L values allow better distribution of the incident radiation through the crop canopy and have increased RUE compared to crops with higher k_L values (Green, 1989; Mirales and Slafer, 1997; Muurinen and Peltonen-Sainio, 2006; Estrada-Campuzano et al., 2012).

Lower RUE values have been related to low LAI values in modern two- and six-row barley cultivars (Muurinen and Peltonen-Sainio, 2006), possibly due to light saturation of most leaves (Sinclair and Horie, 1989). Based on intercepted solar radiation, reported values for RUE are 0.98 to 1.60 g MJ^{-1} (these values would be approximately doubled if they were calculated based

on intercepted PAR) for a wide range of wheat varieties and abiotic environments (Kemanian et al., 2004 and references therein). For wheat, RUE values obtained in experiments conducted on the Canadian Prairies (Lethbridge, AB) across years, irrigation, and cultivars ranged from 0.84 to 4.46 g MJ^{-1} (Major et al., 1992). For barley, the reported RUE values range from 1.02 to 2.52 g MJ^{-1} across a wide range of level, timing, and duration of drought-imposed stress treatments (Jamieson et al., 1995b; Tabarzad et al., 2016). For triticale, the reported RUE values, based on intercepted PAR and averaged over a wide range of cultivars, are from 3.7 to 2.6 and from 3.7 to 2.4 g MJ^{-1} for pre- and post-anthesis periods, respectively (Estrada-Campuzano et al., 2012).

ii. Genotypic differences

Muurinen and Peltonen-Sainio (2006) reported that differences in RUE between temperate cereal species or cultivars within species at high latitudes do exist, but are relatively small and often insignificant. An exception to that finding was the difference in RUE between old and modern six-row barley cultivars: the latter showed significantly higher RUE compared to the old ones. Similarly, Kemanian et al. (2004) reported non-significant barley cultivar effects within the year of cultivation and SD. In Argentina, comparisons between old and modern wheat cultivars revealed differences in cultivar RUE, but mainly in the post-anthesis period. In contrast, in the UK, wheat genotypic variation RUE has been documented and related to pre- and post-anthesis periods and k_L values (Green, 1989). In triticale, RUE has been reported to differ over a wide range of cultivars in both pre- and post-anthesis periods, possibly due to differences in phenological development (Estrada-Campuzano et al., 2012). RUE values based on intercepted solar radiation for old and modern wheat cultivars in Argentina ranged from 0.98 to 1.25 g MJ^{-1} and from 0.37 to 1.02 for pre- and post-anthesis periods, respectively (Calderini et al., 1997). In Mediterranean wheat, RUE values for cultivars released in different eras ranged from 0.45 to 1.08 g MJ^{-1}, from 1.15 to 1.97 g MJ^{-1}, and from 0.39 to 1.54 g MJ^{-1} for the three phenological phases between crop emergence, jointing, anthesis and maturity, respectively (Acreche et al., 2009). RUE values for barley cultivars based on intercepted solar radiation ranged from 0.85 to 1.31 g MJ^{-1} across years, SDs and plant densities (Kemanian et al., 2004). RUE values for old and modern temperate cereal cultivars receiving no nitrogen fertilizer at a high latitude ranged from 1.45 to 2.04 g MJ^{-1} in wheat, from 1.58 to 1.67 g MJ^{-1} in two-row barley, from 1.67 to 2.35 g MJ^{-1} in six-row barley, and from 1.52 to 1.71 g MJ^{-1} in oat (Muurinen and Peltonen-Sainio, 2006). RUE values for a diverse group of triticale cultivars at two irrigation treatments ranged from 2.2 to 4.6 and from 1.5 to 5.0 g MJ^{-1} in pre- and post- anthesis periods, respectively (Estrada-Campuzano et al., 2012).

iii. Seeding date

Reports in the literature on the effect of SD on RUE are scarce and inconclusive. For instance, Miralles and Slafer (1997) reported differences in pre-anthesis RUE values between SDs for standard and semi-dwarf height wheat cultivars, but the results contrasted between the two years of study. In Washington, USA, an early SD (late April) resulted in a 21% higher RUE compared to a late SD (early June) in barley with RUE values, based on intercepted solar radiation, ranging between 1.17 and 0.93 g MJ^{-1}, averaged over cultivars and planting densities, respectively (Kemanian et al., 2004). In contrast, in Pakistan, a late SD (December) resulted in a 18% higher RUE compared to earlier seeding (early November) in wheat, with RUE values ranging between 4.0 and 3.3 g MJ^{-1}, respectively (Wajid et al., 2004).

iv. Temperature

The RUE for barley cultivars was positively correlated with minimum air temperature (Goyne et al., 1993). Kemanian et al. (2004) reported a negative correlation between RUE and temperature in the 23-28°C range.

2.2.7.3 Biomass production as determined by IPAR and RUE

At high latitudes, rainfed temperate cereal crops have low LAI values, especially with low nitrogen fertilizer application rates. Combined with lower solar radiation levels from the middle of the summer onwards, these do not allow for high IPAR. Thus, lower biomass production seems more related to low IPAR than to RUE, which generally has higher values (Muurinen and Peltonen-Sainio, 2006). In other environments, stress-induced biomass reductions in barley are mainly due to reductions in LAI, except when drought is imposed early after crop emergence when RUE reductions are larger (Jamieson et al., 1995b). In triticale, drought conditions negatively affect biomass production mainly due to reductions in RUE (Estrada-Campuzano et al., 2012), although reductions in IPAR may also be responsible if drought is imposed during canopy development (Jamieson et al., 1995b).

2.2.8 Biomass, grain yield and grain yield components

The existence of a plant and the onset and the completion of its life cycle is determined by the prevailing environmental conditions (eg, temperature, water availability, incident radiation, and day length) under which it germinates, grows, and develops. The grain yield of small grain temperate cereals is formed throughout most of the crop growth period (Slafer and Rawson, 1994) and therefore is strongly affected by the environment. Grain yield of temperate cereals has been extensively studied by means of its numerical components (eg, inflorescence number

per unit of cultivated area, seed number per unit of cultivated area inflorescence^{-1}, and average seed weight) (eg, Fischer and Mauer, 1978).

i. Water availability

Harvest index

In Mediterranean-type environments, water availability during crop growth and development may vary and usually becomes smaller towards the end of the crop growth cycle. When higher amounts of rainfall occur prior to anthesis, relatively high grain yields are produced (Austin et al., 1998a and b; Cossani et al., 2009). However, grain yield will also depend on the water availability during the grain filling period, which, under Mediterranean-type environments, often coincides with drought that potentially reduces the grain yield and HI. In contrast to Mediterranean-type environments, at high latitudes, rainfed temperate cereal crops show increased HIs when early season drought results in low vegetative biomass, but later precipitation during the grain filling period results in high grain weight relative to biomass, therefore increasing the HI, but not necessarily the grain yields (Peltonen-Sainio et al., 2008).

Variations in grain yield due to water stress compared to irrigated treatments were mainly attributed to post- anthesis crop growth due to sink strength differences among treatments in a single cultivar each of bread wheat, durum wheat, and barley (Cossani et al., 2009). In other studies, reduced grain yield due to water stress was related more to reductions in total biomass than reductions in HIs in triticale (Giunta et al., 1999; Estrada-Campuzano et al., 2012) and a wheat cultivar (Estrada-Campuzano et al., 2012). Estrada-Campuzano et al. (2012) reported greater HI reduction induced by post- anthesis (Mediterranean-simulated) water stress compared to that caused from pre- anthesis (monsoonal-simulated) water stress. Two triticale cultivars showed contrasting responses in monsoonal-simulated water stress (Estrada-Campuzano et al., 2012).

Inflorescence number per unit land area, grain number per unit land area and inflorescence^{-1} and average grain weight

Under Mediterranean-type environments, the grain yield of rainfed temperate cereal crops is positively correlated to the amount of rainfall the crops receive during the stem extension phase (Cossani et al., 2009 and references therein). The yield component with the largest sensitivity to such conditions is the grain number per unit land area (for a series of temperate cereal species: Fischer and Mauer, 1978; for bread and durum wheat and barley: Cossani et al., 2009 and references therein; for barley: Francia et al., 2011; for triticale: Estrada-Campuzano et al., 2012). The number of spikes is also affected (in bread wheat and in two-row barley: Prado

et al., 2017; in durum wheat: Giunta et al., 1993; in triticale: Estrada-Campuzano et al., 2012), though not quite commonly in barley, especially in two-row barley, due to its relatively lower plasticity (García del Moral et al., 2003). If water stress is imposed in the post-anthesis period during the grain-filling process, grain weight is mainly reduced, relative to non-water-stressed treatments (Fischer and Mauer, 1978 and references therein; for triticale: Estrada-Campuzano et al., 2012). Grain weight is also slightly reduced with increased yields and therefore with higher grain number per unit land area at higher levels of water availability (Siddique et al., 1989; Slafer and Andrade, 1993; Slafer et al., 1996). This reduction is the result of a higher number of grains per unit of land area occurring with a simultaneous increase in the proportional contribution of grains that are constitutively of smaller size and not due to competition (Slafer et al., 1996) such as those derived from distal florets (Acreche and Slafer, 2006) and/or tillers.

Grain number spike^{-1} in wheat closely relates to spike dry weight at anthesis (Fischer, 1985), which, in turn, is related to the assimilate availability during its growth. This is the result of higher fertile floret number (Gonzalez et al., 2011a and references therein) regardless of the causal factor (ie, Fischer and Stockman, 1980; Fischer, 1985; Siddique et al., 1989; Fischer, 1993; Miralles et al., 2000). Crop responses to water stress, with respect to radiation interception and assimilation (eg, lower LAI, higher leaf canopy temperature, less stomatal function) could influence the number of grains spike^{-1}. Water stress has been shown to negatively affect the number of grains per spike in triticale, especially under lower nitrogen levels. Such a response might be affected by the relationship between floret development fertility and assimilate availability during spike growth (Estrada-Campuzano et al., 2012).

i. Genotypic effect

Harvest index

Plant breeding has modified the pattern of distribution of the biomass produced by the plants of newer cultivars compared to older ones. Selection for shorter culms allow more phytomass to be distributed to other parts of growing plants, such as the inflorescence (Calderini et al., 1999; Hay and Porter, 2006), or may allow for increased stored reserves, which could be used during later phenological phases such as the period of grain filling. Indeed, this strategy has been successful in most of temperate cereals species. For instance, wheat lines carrying the *tin* gene bear heavier spikes at anthesis (Duggan et al., 2005a) and have higher HIs (Duggan et al., 2005b). However, since newer cultivars in many parts of the world have reached near optimum culm heights (ie, the relationship between crop height and yield is described by a second order polynomial model), opportunities in targeting higher yields by further reducing plant height could depend on the current degree of the culm height reductions achieved (Slafer et al., 2005).

Wheat and other temperate cereals are cultivated at a wide range of latitudes due to a continuous improvement in their adaptation. The phenology of these species has been crucial to their adaptation with regards to sustainable yield production. Plant breeding has modified the length of the crop life cycle to match the seasonal weather patterns, which has improved crop adaptation. Therefore, adapted cultivars or genotypes in Mediterranean-type environments are characterized by earliness in order to escape water stress that often coincides with later phenological phases (late reproductive or grain filling). Consequently, the grain yield of the species is stabilized and/or increased. Both the plant height reductions and matching phenology with seasonal weather patterns have been successfully implemented in many temperate cereals and account for stabilized and/or higher HIs.

Inflorescence number per unit land area, grain number per unit land area and inflorescence^{-1} and average grain weight

Hay (1995) reported that the higher HIs of modern wheat varieties are the result of higher number of inflorescences per unit land area and higher grain number per spike. Steinfort et al. (2017) reported that spring isogenic lines with lower vernalization requirements (more VRN spring alleles) had higher grain yields (up to 33%) than winter lines. Higher grain yield, which increased along with biomass, was related to grain number m^{-2} and spike^{-1} while the HI of the spring isogenic lines was up to 14% higher than winter lines at recommended SDs, despite a higher spike number m^{-2} for the winter lines. However, in the same study, isogenic lines from the same background carrying the photoperiod sensitivity allele at the PPD-D1 locus showed less clear effects on yield or grain number when seeded at different dates. In other studies, wheat lines missing the *tin* gene bore heavier spikes at anthesis (Duggan et al., 2005a) and produced more grains (Duggan et al., 2005b). The lower grain weight in wheat, which is often associated with increased grain yields is affected by environmental (ie, water availability, seeding date and nitrogen rate) and genetic factors as well as their synergistic effect (Acreche and Slafer, 2006).

ii. Temperature

Temperature strongly affects the growth and development of cereal plants throughout their life cycle, and thus affects grain yield and its components. For early reproductive stages (ie, formation of floral primordia), low, freezing temperature deleteriously affects wheat reproductive tissues due to their relatively high susceptibility at those growth stages (Single, 1985). Higher temperature and/or lower values of the integrative environmental variable photothermal quotient (PTQ) (ie, PTQ = ΣIPAR / Σ (T_{mean} - T_{base})) negatively affects grain yield components in small grain temperate cereals during pre-anthesis phases starting from the DR stage (eg, Rawson and Bagga, 1979; Fischer, 1985). At later reproductive stages (ie, heading

or anthesis), the inflorescence, which is no longer protected by leaf or stem tissues, may be damaged when exposed to low, freezing temperatures (Single, 1985). In addition, episodes of high temperatures or extended warm maximum temperature near anthesis may decrease yields in wheat (Wheeler et al., 1996; Ferris et al., 1998). Finally, temperature is the primary abiotic factor determining grain filling duration; relatively lower temperatures increase the duration (Slafer and Rawson, 1994 and references therein) while freezing temperatures shorten the duration in short-growing-season crop production systems. Examples of the effects of temperature or its combined effect with intercepted radiation on temperate cereals grain yield and its components are outlined below.

Harvest index

Sayre et al. (1997) reported that grain number per unit land area, and therefore the grain yield, in a series of bread wheats correlated to PTQ, but was not related to HI, which only showed a small variation across the years of the study (39.5-41.9%). In another study, reduced grain number per unit land area for a single wheat cultivar positively correlated to the PTQ in a period preceding anthesis (ie, the period of high inflorescence biomass accumulation) while the HI was also reduced by 9% in a shaded treatment compared to the unshaded control (Savin and Slafer, 1991). High temperature episodes near anthesis may reduce the grain number $spike^{-1}$ in wheat and subsequently HI (Wheeler et al., 1996).

Inflorescence number per unit area, grain number per unit area and per inflorescence, and average grain weight

Spikelet and grain number per unit land area is associated with temperature or PTQ for a critical period prior to anthesis in wheat (Rawson and Bagga, 1979; Fischer, 1985; Rawson and Richards 1993; Margin et al., 1993; Cossani et al., 2009) as well as barley and durum wheat (Cossani et al., 2009), when considering both limiting (eg, Margin et al., 1993) or non-limiting (Fischer, 1985; Cossani et al., 2009) conditions for crop growth. For instance, PTQ for twenty five days prior to anthesis, in experimental sites where wheat crops had a low possibility of suffering from water, hail, or biotic stresses, accounted for 52% of the total variability in kernel number and was strongly positively correlated with grain yield. In addition, Cossani et al. (2009) reported that PTQ during the critical growth period, from twenty days prior to, to ten days after anthesis, accounted for 84%, 56%, and 64% of the variation in grain number in bread wheat, durum wheat, and barley, respectively.

When considering the effect of temperature *per se* on grain number per unit land area, the latter has been reported to be negatively related to temperature {(4% reduction in grain number $°C^{-1}$ at 15 °C (Fischer, 1985)} or more weakly related to temperature than that reported for the

quotient (Margin et al., 1993). Grain weight in a series of bread wheats was reported to be negatively correlated to mean temperature during grain filling within a narrow temperature range (18.8-21.6°C) (Sayre, 1997).

iii. Photoperiod

The effect of photoperiod on grain yield and yield components is mainly indirect. Loskutov, (2001) reported substantial inflorescence sterility in oat plants from accessions for which apparent low-temperature vernalization (or photoperiod sensitivity) requirements were not fully met as determined by extremely delayed heading. At high latitudes (eg, the northern grain production belt of North America), photoperiod insensitivity accounts for earlier transition to reproductive development and therefore escape from the coincidence of anthesis and/or grain filling periods with episodes of high temperatures, drought stress, or an early fall killing frost. On the other hand, considering relatively warmer spring temperatures associated with climate change, photoperiod sensitivity may potentially increase the growing period due to the photoperiod requirement for the transition to reproductive development with a potential concomitant increase in the assimilate production and therefore grain yields (Dyck et al., 2004; Lanning et al., 2012). Lower photoperiod sensitivity has been related to increased duration of stem elongation. Usually, the onset of stem elongation coincides with a rapid increase in the inflorescence growth, therefore, stem and inflorescence strongly compete for assimilates. With longer growing seasons, increased stem elongation duration may increase the assimilate production and availability to spike (in shorter-culm genotypes), which may increase the number of fertile florets at anthesis and the grain number spikelet^{-1} (Gonzalez et al., 2011a and b).

Grain yield and its components are not determined exclusively by the main stem. The contribution of tillers to cereal crop grain yield depends on the abiotic environment, including the photoperiod. Long, inductive photoperiods at high latitudes or late SDs at lower latitudes can control tillering of temperate cereals. Tillering is depressed by shorter vegetative phases (Peltonen-Sainio et al., 2009; Steinfort et al., 2017) or enhanced when vernalization and/or photoperiod requirements are not fulfilled, which prolongs vegetative phases (Steinfort et al., 2017). Nevertheless, either of the responses under long photoperiods decrease the contribution of tillers to grain yield via reduced tillering or high tiller mortality.

iv. Seeding date

Different SDs in both Mediterranean- and continental-type environments usually expose the crops to different environmental conditions. Whether a genotype alters its individual phases and/or total growth cycle as a response to different seeding dates depends on its sensitivity to

vernalization and photoperiod (ie, allelic combination of loci that control the response to vernalization and photoperiod). Genotypes with insensitivity to vernalization and photoperiod usually show less modifications in their cycle length and/or individual phenological phases (Steinfort et al., 2017), which mainly occur as responses to temperature (Ugarte et al., 2007) and water, or nutrient availability (McMaster, 1997; McMaster and Wilhelm, 2003; Salvagiotti and Miralles, 2007; Estrada-Campuzano et al., 2008). Optimal, or recommended, SDs normally yield better than late SDs (eg, Lanning et al., 2012). Later SDs often coincide with higher temperatures and longer photoperiods. These conditions increase the growth cycles and/or individual phenological phases if vernalization requirements are not fulfilled (Whitechurch et al., 2007) or decrease them due to photoperiodic sensitivity up to optimum photoperiod values (Alzueta et al., 2014) in terms of chronological and Tt. Delayed fulfillment of vernalization requirements (Steinfort et al., 2017) and the lower pre-anthesis PTQ (eg, Rawson and Bagga, 1979; Fischer, 1985; Savin and Slafer, 1991) have negative effects on grain yield and its components.

Harvest index

Under optimal growing conditions, SDs have little effect on the HI of crops (Hay, 1995). However, when stress is imposed, HI negatively correlates to longer growing periods and later maturity in wheat due to frost, lodging (Stapper and Fischer, 1990), or stress during or near the end of the growing season (Hucl and Baker, 1987). Contrasting SDs caused water stress and delayed phenological development, which reduced HI, for spring wheat (Hucl and Baker, 1987), durum wheat (Giunta et al., 1993) and triticale (Estrada-Campuzano et al., 2012)

Steinfort et al. (2017) reported that the response of grain yield and yield components in wheat isolines differing in photoperiod sensitivity were inconsistent. The lower grain weight in wheat, often associated with increased grain yields as described earlier with respect to higher water availability or genotypic variation or their synergistic effect, holds for the SD effect as well (Acreche and Slafer, 2006 and references therein).

Chapter 3 A leaf-development-based phenological scale for annual canarygrass

3.1 Introduction

The development of cereal species or genotypes within species are often compared when grown under the same or different environmental conditions. Leaf-development-based phenological scales, such as the Haun Scale (Haun, 1973), are often used to determine differences in leaf-development stages. The Haun Scale is expressed in rational numbers: the integral part denotes the number of the leaf laminae that have fully expanded and the fractional part denotes the length of the youngest expanding leaf lamina as a portion of the length of the preceding leaf. The Haun leaf stage (HLS) is expressed as follows:

$HLS = (n-1) + (L_n / L_{n-1})$ (McMaster, 1997) (Equation 3.1)

where n is the number of visible leaf tips, L_n is the length of the youngest leaf lamina, and L_{n-1} is the length of the second youngest leaf lamina (often the last fully expanded leaf lamina). The Haun Scale has been developed for wheat. Sonego et al. (2000) demonstrated that the scale can also be used to calculate leaf stages for oat plants despite the simultaneous expansion of two consecutive main stem leaf laminae above their preceding, enclosing leaf. In that case, the length of the reference leaf that is used to calculate the HLS is lower than its ultimate length, so the HLS is somewhat overestimated.

Casual observations of the main stem leaves of field-grown canaryseed plants suggest that their development pattern is similar to that of oat leaves. Specifically, before a main stem leaf, leaf n, reaches its ultimate length, there is at least a second leaf, leaf n+1, whose tip is visible above its insertion point of the enclosing leaf n. That leaf-development pattern does not hold for wheat plants (Kirby, 1994), where the tip of a main stem leaf appears approximately at the time when the preceding leaf has finished its extension, determined by the appearance of its leaf ligule. Apart from that, casual observations of field-grown canaryseed plants suggest that the flag and penultimate leaves are shorter than the preceding leaves. Thus, the Haun Scale could underestimate the plant leaf stages because the ultimate length of the reference leaf would be too long relative to the youngest leaf.

The differences between wheat, oats, and canaryseed could affect plant-growth-stage calculations using leaf-development-based phenological scales developed for wheat. In addition, slightly different leaf scales such as those suggested by Sonego et al. (2000) for oat could generate artifacts and not true differences in leaf stage determinations. Therefore, the objective of this experiment was to determine whether there is deviation, and if so its magnitude in the comparison of different leaf-development-based scales and to develop an appropriate

leaf-development-based scale for canaryseed. The scale must determine the leaf stage of canaryseed with accuracy to be used to compare plant development in the present as well as in subsequent studies. The leaf scale should also be simple or easily generated from an existing scale.

3.2 Materials and methods

3.2.1 Plant material

The glabrous canaryseed cultivar used in this study was CDC Bastia, which was developed at the University of Saskatchewan Crop Development Centre in Saskatoon, Canada. In tables and figures, the cultivar name may appear without its acronym CDC due to space limitations.

3.2.2 Growing conditions

The experimental plots were sown on fallow land in the Investigation Field (University of Saskatchewan campus) in 2013 and 2014. The soil was a dark brown clay, clay-loam.
Chemical analysis of the top 60 cm of soil conducted at the end of the growing season in the autumn of the previous year showed NO_3^--N levels of 9.1 and 3.8, P levels of 5.4 and 3.3 and K levels >67.3 and >60.5 g m^{-2}, corresponding to 2013 and 2014 growing seasons, respectively. In both years, experimental plots were supplemented by 5 g m^{-2} (50 kg ha^{-1}) of the product 28-23-0 [N-P-K-S] ESN. Weeds were removed either by hand or using hoes. When needed, Buctril M (Bromoxynil and MCPA) was sprayed at half of the recommended rate. No fungicides or insecticides were used throughout the crop cycles, but no serious spread of disease or damage from insects was observed.

3.2.3 Experimental set-up

The present experiment is part of a study where five cultivars were seeded on different dates in two consecutive years. Two replications of the three SDs, an early, a late and a very late (or v.late due to space limitations) were randomly assigned to two blocks of an RCBD with the SD being the main plot. The cultivars were randomly assigned within each main plot in each of the four complete replications within each SD. The experiment consisted of 120 plots resulting from 3 SDs × 5 cultivars × 4 replications $block^{-1}$ × 2 blocks.

Each plot consisted of ten rows 4.0 m long, spaced 20 cm apart seeded at the rate of 200 seeds m^{-2} using a seeding depth of approximately 3 cm. The two outer rows of each plot were used as borders and measurements were conducted on seedlings from the six inner rows. Each plot was divided into several subplots. The data used for the present experiment were from one

subplot located in the center of the plot, which facilitated *in situ* observations. Each subplot occupied 0.7 m^2 (0.58 m along the rows and 1.2 m across the rows).

The three SD targets were early May, late May and mid-June. The actual SDs depended on when weather and soil moisture permitted seeding and these were, for 2013, 8 May, 27 May and 28 June, and for 2014, 9 May, 2 June and 25 June.

3.2.4 Observations and estimates

Few plants in total, but never more than two $plot^{-1}$, senesced before reaching physiological maturity. *In situ* observations made on those plants were omitted during the data analysis.

3.2.4.1 Leaf-development-based scales

To better estimate the actual leaf stage of canaryseed plants, the Haun Scale could be modified to compare the actual laminae length (ALL) of the two youngest expanding leaves with their respective ultimate laminae length (ULL). Weightman et al. (1997) used a similar method to calculate the leaf stage of a wheat plant, though for the last visible leaf lamina only. In this case the leaf stage is calculated from the Haun leaf scale, which is modified based on the ALL and ULL of the two youngest leaves. Thus, the estimated leaf stage will be abbreviated as modified Haun leaf stage ($MHLS_{2YL}$) and calculated as:

$MHLS_{2YL} = (n-2) + (ALL_{n-1} / ULL_{n-1}) + (ALL_n / ULL_n)$ (Equation 3.2).

Given the main stem-leaf-appearance pattern of canaryseed, such a function may generate actual main stem-based seedling leaf stages based on the Haun or modifications of the Haun scale. However, a modified Haun scale might not generate precise phyllochron estimates. Phyllochron, being the time (or Tt) between the appearance of two successive leaf tips, might be overestimated; thus, the Haun scale would be a more appropriate leaf-development-based scale. Given the uncertainty in using the Haun scale to determine canaryseed leaf stage, a slightly modified Haun scale ($MHLS_{YL}$), like the one already suggested, may be more accurate. The decimal part of the leaf stage according to this scale is based on the actual and ultimate lamina length of the youngest leaf. The proposed leaf scale would more accurately estimate phyllochron, and would be less likely to overestimate the plant leaf stage to the extent that the Haun Scale might.

To determine the exact leaf stage of canaryseed plants, the Haun scale may be modified again to compare the ALL of all leaves with their respective ULL. In this case the actual leaf stage (ALS) is calculated as:

Actual leaf stage (ALS) = $\sum (ALL_i / ULL_i)$ i=leaf 1, leaf 2…., flag leaf (Equation 3.3)

To produce a leaf scale for canaryseed development that would serve the needs mentioned above, both simple linear and polynomial regression analyses between the observed data from the two methods, the Haun and the modified method (based on the two youngest leaves), were conducted. The models generated to predict the ALS from the HLS are presented in Table 3.1. The results of the comparison of the two modifications of the Haun scale, the MHLS and the ALS, are also presented. Any difference between MHLS and ALS indicate that at least the lamina of leaf n-2 or even its precedent still expand despite the appearance of the leaf n tip.

For the leaf-scale comparisons, the individual leaf lamina length of the three youngest leaves was regularly (two to four but usually three times per week) recorded *in situ* on six plants per plot that were randomly selected and tagged within the subplots. That procedure was followed to determine the magnitude of the bias on the comparison of the different scales for phenological development.

3.2.4.2 Weather data

Rainfall and temperature records were obtained from the weather stations at the Horticulture Field Station of the University of of Saskatchewan and the Saskatchewan Research Council, located one and two kilometers from the experimental site, respectively. The daily accumulated thermal time in growth degree-days was calculated as the average of the daily maximum and minimum temperatures using a base temperature of zero degrees centigrade. Temperatures below zero were considered as zero. The air temperature, rainfall, Tt, and incoming solar radiation throughout the plant growth period is presented in Figure 3.1.

3.3 Results

CDC Bastia plants had more than one leaf lamina extending at the same time in all three SDs and both years (Figure 3.2). One way to determine the exact number of leaf laminae extending simultaneously is to extrapolate the curve of the leaf lamina length back to the thermal time axis in order to estimate the time that the leaf tip of each leaf appeared using a sigmoid function. Alternatively, comparing the ALS and HLS would determine if only the youngest leaf, or older ones, extend simultaneously

The difference between the HLS and the ALS ranged from -0.3 to +0.6, indicating that HLS mainly overestimates the ALS and that care must be taken in selecting the scale used to determine the leaf stage of canaryseed plants. Comparing the ALS and $MHLS_{2YL}$ generated differences which ranged from -0.01 to +0.03 leaves, indicating that the leaf n-2 had almost finished its expansion by the time that the tip of leaf n had appeared above its insertion point of the enclosing n-1 leaf lamina.

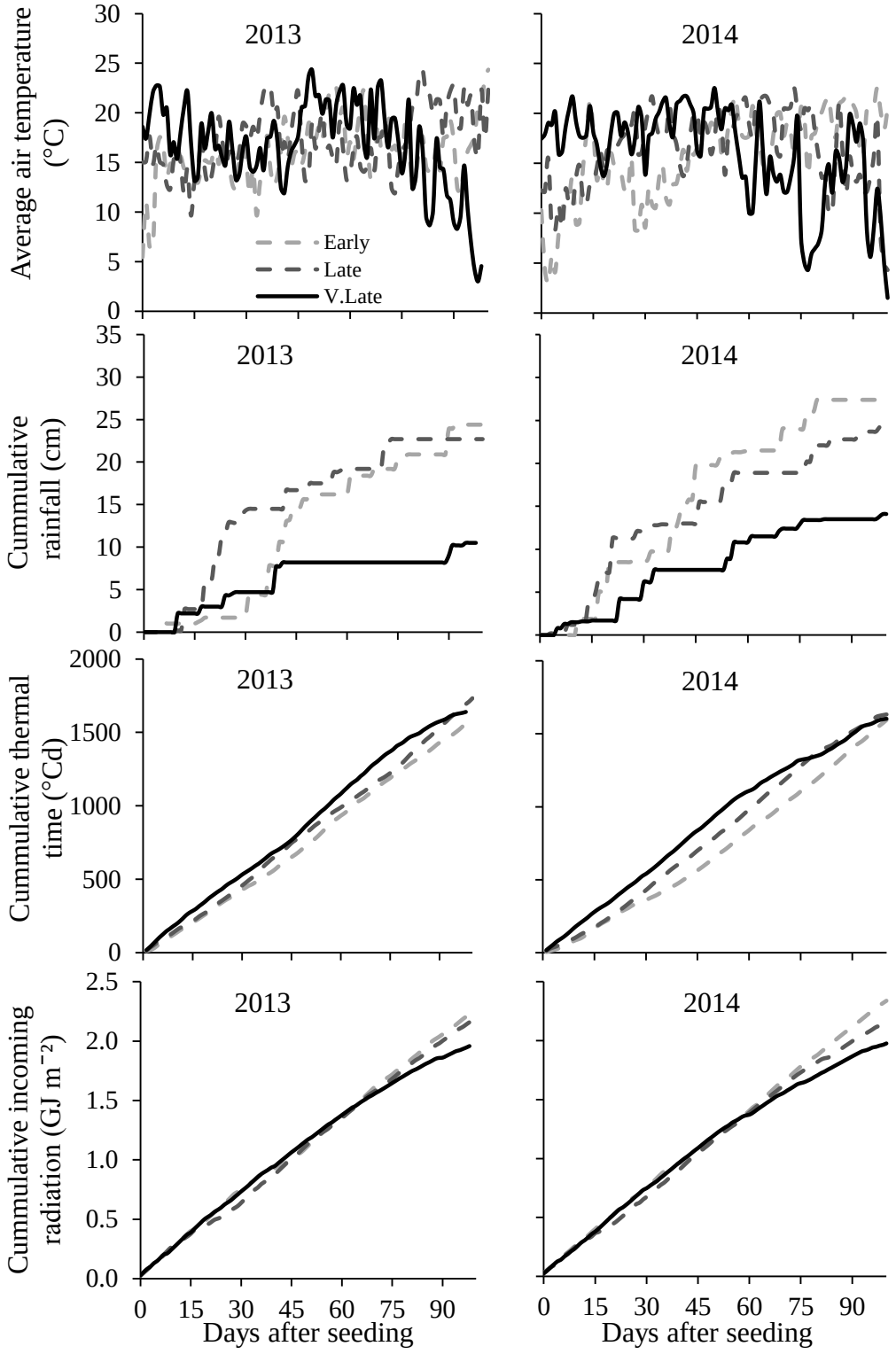

Figure 3.1. Daily average air temperature, cumulative rainfall, cumulative thermal time and cumulative incoming radiation from seeding throughout the growth cycle of the crops. For curves color, see legend at the top of the figure.

Table 3.1. Temperature, rainfall and thermal time averaged over month and for the entire crop season (May-September) for 2012, 2013 and 2014.

Month/Period	Year			30-year average
	2012	2013	2014	
Temperature °C (Deviation from 30-year month average)				
May	9.8 (- 2.4)	13.0 (+0.8)	10.1 (- 2.1)	12.2
June	15.6 (- 1.0)	15.5 (- 1.1)	14.0 (- 2.6)	16.6
July	19.6 (+0.5)	17.3 (- 1.8)	18.3 (- 0.8)	19.1
August	17.8 (- 0.2)	19.0 (+1.1)	17.9 (- 0.1)	18.0
September	13.4 (+1.2)	14.9 (+2.7)	12.3 (+0.1)	12.2
Deviation from 30-year May-September average	- 0.4	+0.3	- 1.1	15.6
Rainfall (mm) (Deviation from 30-year average)				
May	143[1](+93)	17[2](- 33)	85[3](+35)	50
June	97 (+37)	135 (+75)	121 (+61)	60
July	82 (+19)	47 (- 16)	72 (+ 9)	63
August	66 (+23)	35 (- 8)	39 (- 4)	43
September	1 (- 31)	20 (- 12)	20 (- 12)	32
Deviation from 30-year May-September average	+141	+ 6	+89	248
Thermal time °Cd (Deviation from 30-year average)				
May	304 (- 72)	379 (+ 3)	296 (- 80)	376
June	475 (- 24)	472 (- 27)	422 (- 77)	499
July	612 (+17)	531 (- 64)	570 (- 25)	595
August	549 (- 12)	588 (+27)	549 (- 12)	561
September	397 (- 28)	439 (+70)	368 (- 1)	369
Deviation from 30-year May-September average	- 63	+ 9	-195	2400

Note: [1] 81 mm prior to seeding; [2] 1 mm prior to seeding; [3] All rainfall occurred after seeding;

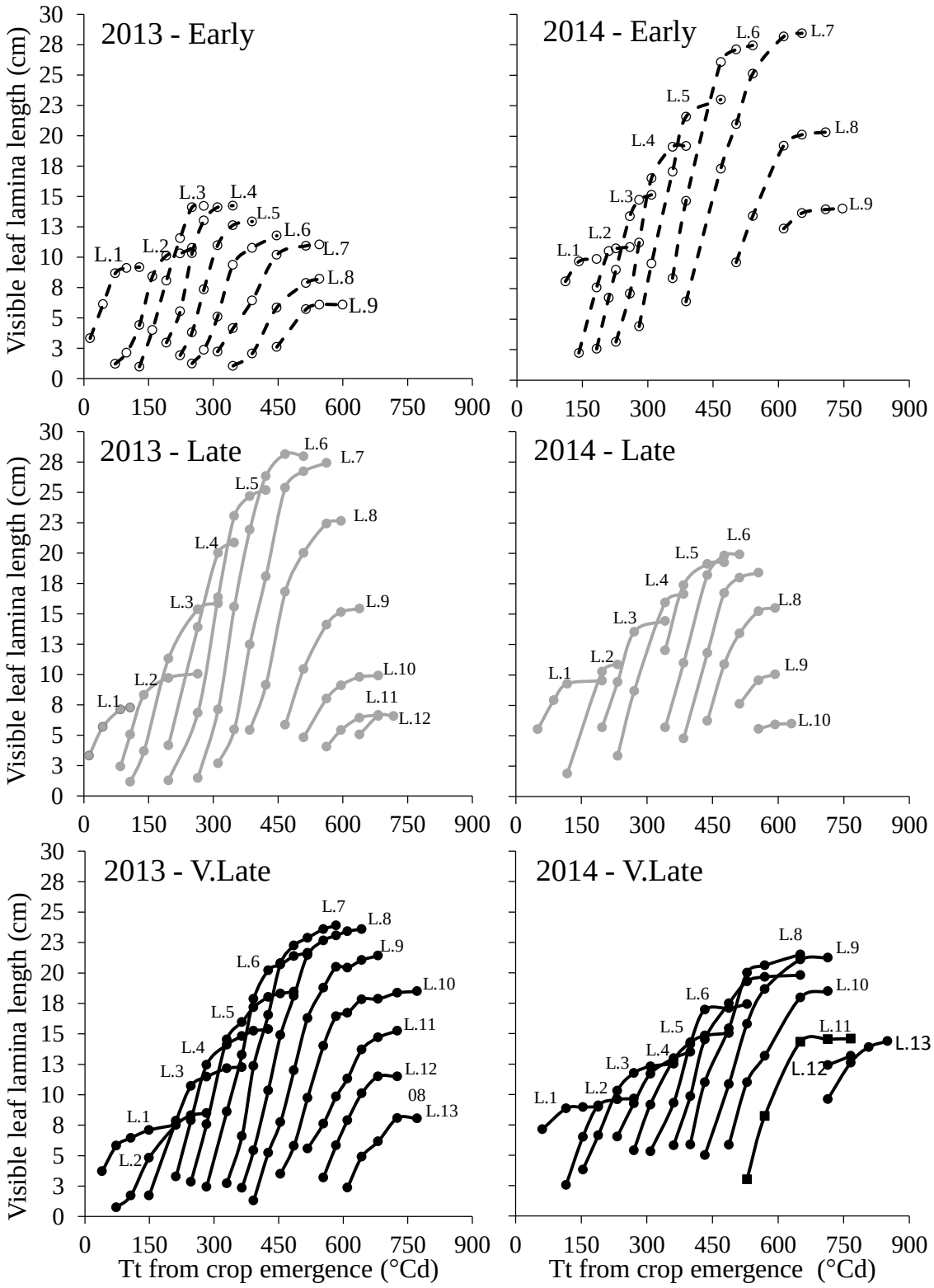

Figure 3.2. Mean visible main stem leaf lamina length versus the thermal time (Tt) elapsed from crop emergence for the canaryseed cultivar CDC Bastia when seeded early, late and very late in 2013 and 2014, respectively. Each data point is derived from observations on two blocks seeding date^{-1}, four replications block^{-1} and six plants replication^{-1}. *L.* stands for *Leaf* and the number following it denotes the leaf rank on the main stem.

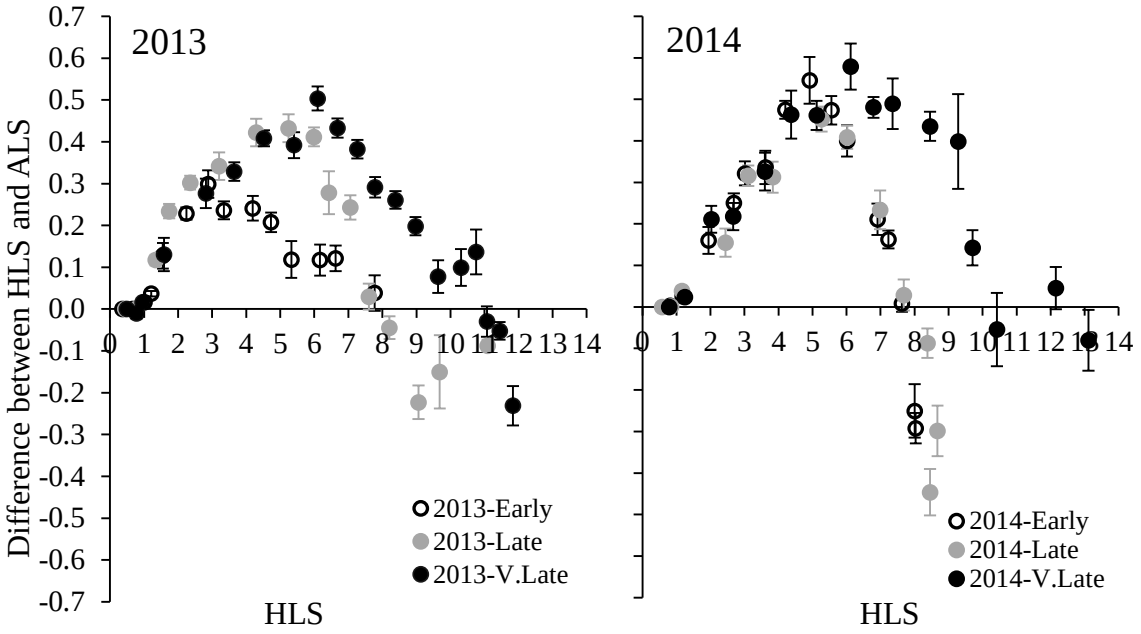

Figure 3.3. Mean difference between the Haun leaf stage (HLS) and the actual leaf stage (ALS) versus main stem HLS for the canaryseed cultivar CDC Bastia when seeded early (open circles), late (grey-closed circles) and very late (black-closed circles) in 2013 (A) and 2014 (B). Mean difference values are derived from observations conducted on two blocks seeding date^{-1}, four replications block^{-1} and six plants replication^{-1}.

In the model equations presented in Table 3.2, the coefficients of the slope are very close to unity. This indicates a very similar variation pattern in leaf stages estimated by the two methods from crop emergence to flag leaf ligule appearance. The intercepts of the equations indicate the average difference in leaf stage between the two methods. Based on the model equations, HLS overestimates the ALS by 0.13 to 0.32 leaf units.

Table 3.2. Simple linear and second order polynomial regressions between actual (ALS) and Haun (HLS) leaf stage estimates[1] obtained for the canaryseed cultivar CDC Bastia when seeded on three dates in 2013 and 2014.

		Linear model			Polynomial model			
Year	Seeding Date	Equation	rMSE	r^2	Equation	rMSE	r^2	df [3]
2013	Early	ALS= -0.131 + 1.008×HLS	0.161	0.997	ALS = 0.0305 + 0.885×HLS + 0.014×HLS^2	0.141	0.998	15
	Late	ALS = -0.277 + 1.025×HLS	0.205	0.997	ALS = 0.012 + 0.854×HLS + 0.016×HLS^2	0.133	0.999	15
	V.Late	ALS = -0.245 + 1.010×HLS	0.199	0.998	ALS = 0.121 + 0.816×HLS + 0.016×HLS^2	0.053	0.999	15
2014	Early	ALS = -0.312 + 1.026×HLS	0.253	0.991	ALS = 0.409 + 0.592×HLS + 0.471×HLS^2	0.089	0.999	14
	Late	ALS = -0.228 + 1.029×HLS	0.262	0.994	ALS = 0.264 + 0.684×HLS + 0.0368×HLS^2	0.110	0.999	12
	V.Late	ALS = -0.315 + 1.009×HLS	0.227	0.997	ALS = 0.131 + 0.815×HLS + 0.014×HLS^2	0.107	0.999	15
Regressions on pooled data[2]		ALS = -0.228 + 1.021×HLS	0.215	0.995	ALS = 0.0736 + 0.829×HLS + 0.020×HLS^2	0.156	0.997	59

[1]ALS and HLS estimates were obtained from observations on two blocks seeding date^{-1}, four replications block^{-1} and six plants replication^{-1}

[2] Data pooled over two years and the first two seeding dates year^{-1}

[3] Degrees of freedom

The pooled observations of ALS and HLS over two years and only the first two seeding dates year^{-1} were used to generate a regression equation (Table 3.2). Coefficients of that function were very close to those estimated for the individual seeding dates, indicating little error in leaf stage determinations using the general function.

3.4 Discussion

The present study was initiated by the casual observations that more than one main stem leaf lamina expand at the same time. The use of an appropriate leaf-development-based scale for canaryseed is discussed herein.

Modifications of the Haun leaf scale, such as the $MHLS_{2YL}$ and $MHLS_{YL,}$ are difficult to use in the field due to the lack of data of ultimate leaf laminae lengths and due to the cost of such data collection. Alternatively, the extensively reported Haun leaf scale can be easily used. The linear and the second-order polynomial functions generated by regression analyses of the pooled observations of ALS and HLS over two years and the first two SDs year^{-1} may be used to calculate the ALS of field-grown canaryseed plants from HLS observations. The data from the very late SDs were omitted from the generation of the scale because those dates in both years were two months later than the recommended dates based on local seeding time practices in central Saskachwean. If the leaf-development pattern of canaryseed is affected by the weather conditions, the extreme SDs theoretically could have affected the accuracy with which the ALS was generated from HLS observations. In practice, however, that would likely have a small impact on the model functions generating ALS from HLS because the coefficients of both the linear and polynomial functions from observations for the very late SDs were not much different from those for the earlier SDs.

$MHLS_{YL}$ estimates were used for the leaf appearance and the tillering pattern as well as the phenological development of canaryseed in the present study. However, regression analyses conducted between $MHLS_{YL}$ and $MHLS_{2YL}$ for each SD separately returned highly significant (P<0.001) functions that explained more than 99% of the variation. Thus, results are expected to be very similar using either of the leaf scales for the leaf stage calculations.

3.5 Conclusion

In conclusion, despite the main stem leaf appearance overlapping in canaryseed, the standard Haun scale or its modification based on the youngest leaf would be sufficient to determine seedling leaf stages, as has been extensively used in primary small grain temperate cereals.

Transition section between Chapter 3 and Chapter 4

The use of an appropriate leaf-development-based scale for canaryseed was the subject of Chapter 3. The objective was to compare different leaf-development-based scales and to develop an appropriate leaf-development scale for canaryseed. The standard Haun scale or its modification based on the youngest leaf would be sufficient to determine canaryseed seedling leaf stages. The objective of the experiments in the next chapter (Chapter 4) is to investigate the impact of seeding time on apical development of canaryseed and to determine if it is related to the species potential low-temperature vernalization requirement or to its leaf-development pattern.

Chapter 4 Impact of seeding time on apical development of annual canarygrass: A case of vernalization requirement?

4.1 Introduction

Phalaris canariensis L., commonly known as annual canarygrass or canaryseed, is a C3 (Smith and Brown, 1973), self-fertilizing (Carlson et al., 1996; Matus-Cádiz and Hucl, 2006), diploid (2n=12) (Matus-Cádiz et al., 2003) small grain temperate species native to southern Europe and the Middle East. Canaryseed grain yield is low compared to other small grain temperate cereals (Miller, 2000), especially when seeded later than at the optimum or recommended SDs (Miller, 2000; Bodega et al., 2003; May et al., 2012a).

Cogliatti et al. (2011) reported that seeding canaryseed accessions over dates and years caused crop cycle differences, in terms of Tt, which were principally related to differences that occurred from crop emergence to heading.

The sensitivity to vernalization and photoperiod of a particular genotype largely determines whether it alters its individual phases and/or the total cycle length as a response to different SDs. Depending on an unmet vernalization requirement or a photoperiodic sensitivity of a genotype, delayed seeding, often coinciding with higher temperatures and longer photoperiods, may lengthen the growth cycles and/or individual phenological phases (Whitechurch et al., 2007) or shorten the cycles until optimum photoperiod values occur (Alzueta et al., 2014), respectively. Consequently, delayed meeting of vernalization requirements (Steinfort et al., 2017) and lower PTQs pior to anthesis (eg, Rawson and Bagga, 1979; Fischer, 1985; Savin and Slafer, 1991) may reduce grain yield and yield components.

Hucl (personal communication, 2012) observed a correlation (r=0.66**) between decreased yields and delayed heading for early-seeded versus late-seeded canaryseed trials. Miller (2000) speculated on an unmet vernalization requirement of the canaryseed cultivar Keet. However, to date, no studies have documented a vernalization requirement for canaryseed. Earlier studies on wheat have shown that partially or fully met vernalization requirements reduced the final leaf numbers (FLNs) on the main stem (eg, Brooking et al., 1995; Mahfoozi et al., 2001a and b; Brooking and Jamieson, 2002). Differences in the FLN have been positively and linearly associated to differences in the Haun stage (HS) of a plant at the appearance of double ridges (DR, the floral primordia in the axils of the leaf primordia) or the stage of floral initiation (HS_{FI}) as well as the stage of terminal spikelet (HS_{TS}) in wheat (Brown et al., 2013 and Jamieson et al., 2007, respectively) and oat (Sonego et al., 2000). Differences in the FLN have also been conversely related to the rate of the basipetal reproductive commitment, which overgrows the

leaf primordia from the middle of the apex in wheat (Brooking and Jamieson, 2002). For canaryseed, such information would be important for documenting a potential vernalization requirement associated with differences in the FLN. Thus, the first objective of this study was to provide information about the potential low-temperature vernalization requirement of canaryseed cultivars.

Casual observations of the leaf development of canaryseed plants suggest that before leaf n reaches its ultimate length, the tip of leaf n+2 may be visible above its insertion point relative to the enclosing leaf n, especially with late-sown crops. Based on the coordination between leaf appearance and expansion and stem apex development in wheat (Kirby, 1990) and oat (Sonego, 2000), the potential simultaneous expansion of leaf lamina above their insertion point of the enclosing leaf sheaths is hypothesized to take place at the leaf primordium expansion zone close to the seedling crown, shortening the time intervals between the start of elongation of two consecutive leaf primordia into extending enclosed leaves. That would mean a faster elongated leaf primordium appearance at the enclosed stem apex. In the dicot cucumber (*Cucumis sativus* L.), the temperature of the apical bud and other plant organs have been associated with the leaf initiation rate (Savvides et al., 2016). If prevailing weather conditions, such as the seedbed temperature, near the seedling crown and/or the photoperiod allows such a mechanism to occur with or without a decreased reproductive commitment at the stem apex, a mechanism that may increase the FLN of canaryseed plants when seeded late in the crop season would arise. For wheat, the increased soil temperature at the crown depth did not increase leaf appearance rates because cell expansion, which largely determines leaf expansion and appearance, is greatly affected by factors other than temperature (McMaster et al., 2003). The hypothesis of the present study mentioned above, however, considers cell growth and expansion at a much smaller scale compared to that of an unfolding leaf, thus precluding the effect of other factors than temperature on the leaf appearance rate. If the hypothesis of the present study is true, the potentially increased FLN with late seeding would likely not be due to an unmet vernalization requirement or it would be the first time in the literature for a vernalization requirement in cereals to be morphologically described. Thus, the second objective of this study was to determine whether a potentially increased FLN on the main stem of canaryseed with delayed SDs was associated with a higher elongated leaf primordium appearance at the enclosed stem apex.

Vernalization requirement, either facultative or obligate, is a common characteristic among species originating from the Eurasiatic part of the Mediterranean region, where canaryseed originates. The cultivar Keet, for instance, originates in Iran. However, more recently bred

cultivars such as CDC Bastia and others, are the result of planned crosses using the first glabrous canaryseed cultivar with the potential for human consumption, namely CDC Maria, which was obtained via mutagenesis from Keet (Hucl et al., 2001a). It is unknown whether mutagenesis has affected the response of the glabrous genotypes to their potential low-temperature vernalization requirement. Thus, the third objective of this study was to determine if different canaryseed cultivars have different low-temperature vernalization requirements and leaf initiation rates.

4.2 Materials and methods

4.2.1 Plant material

The two canaryseed cultivars used in this study, the pubescent-hulled cultivar Keet (Robinson, 1979) and the glabrous cultivar CDC Bastia, were evaluated along with the hard red spring (HRS) wheat cultivar AC Barrie and the spring-type oat cultivar CDC Morrison. The cultivar Keet was selected in Minnesota, USA, as a single plant from an accession from Iran. CDC Morrison and CDC Bastia that were used in the controlled-environment experiment were developed at the Crop Development Centre at the University of Saskatchewan in Saskatoon, Saskatchewan, Canada. CDC Bastia resulted from planned crosses using the first glabrous canaryseed cultivar, CDC Maria, a mutagenesis-derived cultivar from Keet (Hucl et al., 2001a). AC Barrie was developed at the Agriculture and Agri-Food Canada Research Centre in Swift Current, Saskatchewan. Both AC Barrie (McCaig et al., 1996) and CDC Morrison (Canadian Food Inspection Agency, 2018) are photoperiod-sensitive varieties. AC Barrie also has a minimal vernalization requirement (Iqbal et al., 2006). In tables and figures, cultivar names may appear without their acronyms CDC and AC due to space limitations.

4.2.2 Growing conditions - field experiments

For years and location of the field experiments, soil type and chemical analysis, fertilizer application and weeds control see section 3.2.2.

Information regarding the air temperature and photoperiod is presented in figure 4.1. Weather conditions are shown for the period of regularly destructive harvests, the last of which was very close to that stage at least in five out of six year × seeding date combinations. For the remaining year × seeding date combination (ie, 2013-late seeding), when destructive harvests ended well before that stage, the period shown is as on late seeding in 2014.

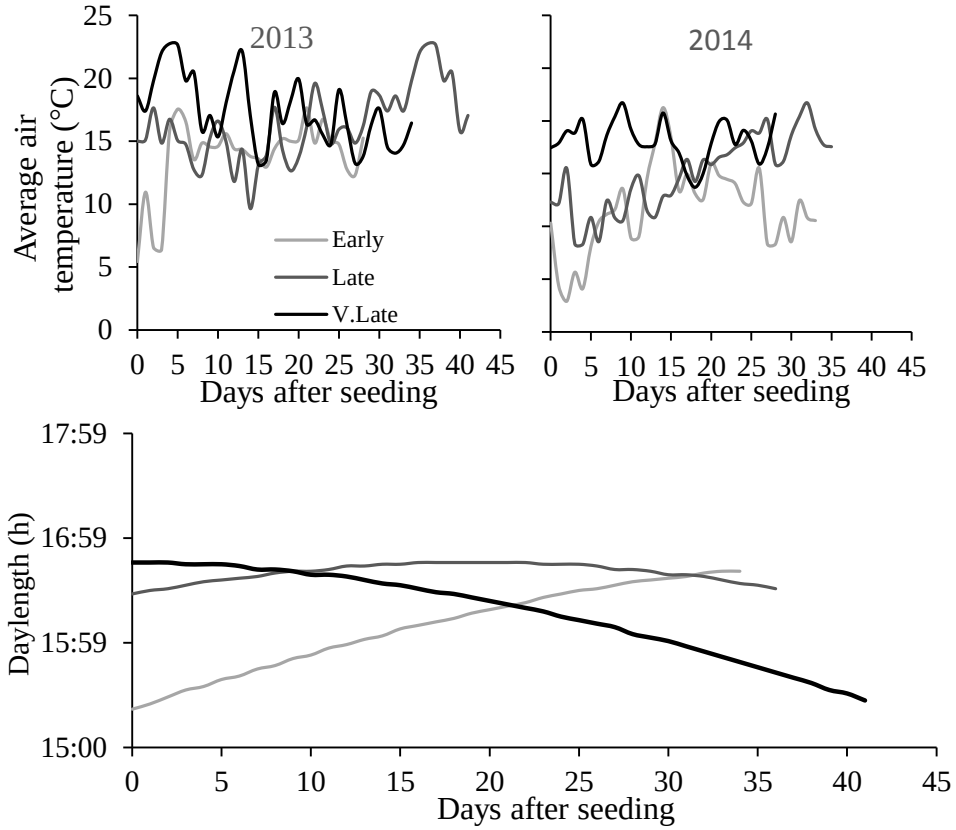

Figure 4.1. Daily average air temperature and daylength from seeding to the date when the last observation was obtained for the canaryseed cultivars CDC Bastia and Keet when seeded early (light-grey line), late (dark-grey line) and very late (black line) in 2013 and 2014.

4.2.3 Experimental set-up

4.2.3.1 Field experiment

For experimental design and seeding practices see section 3.2.3.

In each block × seeding date × replication × cultivar plot, nine subplots were identified. Eight of them served for weekly series destructive harvests and were randomly assigned a number denoting their harvest order (used for purposes beyond the scope of this chapter). The subplot located in the center of the plot facilitated *in situ* observations (used for research questions for this and other chapters). All nine subplots were vertically oriented to the seeding rows. The ground area occupied by each of the eight subplots was 0.24 m^2 (0.2 m along the rows and 1.2 m across the rows) and 0.7 m^2 by the central one (0.58 m along the rows and 1.2 m across the rows). Border subplots of equal size to the numbered ones were maintained between two consecutive numbered subplots as well as in front and after the first and last numbered subplot, respectively.

4.2.3.2 Controlled-environment experiment

The two canaryseed cultivars, a spring wheat cultivar, and an oat cultivar were evaluated for a potential vernalization (exposure of emerged seedlings to low non-freezing temperature) response under controlled-environment conditions. The seeds were initially imbibed and maintained in the dark for 48h at room temperature to ensure homogeneous germination. The seeds were then sown into 3.2-L volume (7.5-cm radius, 17-cm height) plastic pots containing Sunshine Mix no.3 potting mixture (Sun Gro Horticulture, MA, USA) at a density of five seeds per pot. The imbibed seeds grew under a 20h photoperiod at 20°C and a vapor pressure deficit of 0.3 kPa for six days. During the illumination period, the pots received 300 μmol m^{-2} s^{-1} for 8h and 20-30 μmol m^{-2} s^{-1} for 6h prior to and after the 8h period from fluorescent tubes (color 835). After six days, when the seedlings had approximately one leaf fully unfolded, the pots were distributed to growth chambers with air temperatures at 5°C, 10°C, and 15°C, with a 20h photoperiod and a PPFD of 300 μmol m^{-2} s^{-1}. That PPFD level was maintained for 8h each day. For 6h prior and 6h after the 8h period, the PPFD was kept at 15±3 μmol m^{-2} s^{-1} using compact fluorescent light bulbs. Young seedlings were used instead of (imbibed) seeds to ensure that all plants would be exposed to the same photoperiod for the same number of days within each vernalization duration. The procedure described was followed five times, at intervals of seven or five days, so the sown pots stayed in the low-temperature chamber for 0, 2, 7, 14 and 21 days and all vernalization treatments ended on the same day. At the end of the cold treatment, all pots were kept in the chamber until the flag leaf collar appeared. The temperature in the low-temperature chambers gradually increased (over 24h) so that the chamber reached a temperature of 20°C, a photoperiod of 20h, and a PPFD as described for the beginning of the cold treatment.

The same procedure was followed for ten additional smaller pots (approximately 2.5-cm radius, 5-cm height) containing two seedlings each. These pots were regularly removed from the chambers and used for dissections while the remaining pots were rearranged to maintain constant plant density and minimize position effects within the chamber.

All treatments were applied to six pots (experimental unit) containing five seedlings each and the pots were divided in two runs separated either in space (different chambers) or in time with three pots in each run considered as repetitions. The control treatment, for which the plants remained for zero days under vernalizing temperatures, was applied only to the chambers set at 10°C.

4.2.3.3 Short experiment under a controlled-environment

The experimental set-up described above was followed for a short experiment in a controlled environment. Imbibed seeds at room temperature or young seedlings (one leaf stage) were exposed to an 8h photoperiod followed by a 16h dark period for a vernalizing period of 14 days at 10°C. During the post-treatment period, the photoperiod was either 17h or 20h and the temperature was as described for the other vernalizing treatments. This short experiment was conducted to investigate the potential effect of physiological age and that of the post-vernalizing treatment environmental conditions on the vernalization saturation of canaryseed.

4.2.4 Measurements and observations

4.2.4.1 Field experiment

The FLN on the main stems of plants was determined by leaf counting on previously intact, randomly selected and tagged, harvested plants from the central subplot at the final harvest of each plot. Main stem leaves were marked every third or fourth leaf to ensure that the main stem FLN was accurately determined. Means were obtained over the six plants replication^{-1}.

The seedlings needed for dissection were collected from the border subplots commencing from the two outer ones (first and last) assuming no plant competition for resources at early seedling development (up to approximately the third leaf stage) and continuing with other border subplots, according to which the numbered subplots were harvested at each plot. The seedlings were harvested from the inner rows to avoid effects from resources availability and care was taken to ensure that the border subplots from which the seedlings were harvested would not affect resources availability for seedlings of neighboring non-harvested subplots. Given that no documented information is available in the literature regarding canaryseed stem apical development, seedlings harvests for dissection purposes commenced approximately at the first leaf stage and ended well beyond the initiation of the floral primordia except for the 2013 Late-seeded plots when dissections ended soon after the floral primordia had been initiated at the seedlings stem apices. Therefore, the number of harvests ranged from five (2013-early seeding) to nine (2014-very late seeding).

The most advanced seedlings, determined by their leaf stage, were dissected on the day of harvest to obtain information on the stem apical development stage for each treatment, while the rest of the seedlings were stored in a fridge at approximately 3-5°C, covered by moisten paper napkins in the dark, until they were dissected. The leaf stage of the dissected seedlings was determined by the modified Haun leaf stage based on the youngest leaf ($MHLS_{YL}$, the term

MHLS will be used hereafter) as described in Chapter 3 and means were obtained for six seedlings plot^{-1}.

The pseudostems of the seedlings from both field and controlled-environment experiments were dissected under a stereozoom binocular microscope (Nikon, SMZ-2B). Every emerged and emerging leaf as well as every leaf primordium and 1st-order branch primordium (Landes and Porter, 1990) (the term *floral* will be used for the latter primordium hereafter) was recorded. To estimate the leaf initiation rate and leaf primordium initiation rate at the shoot apex, linear regressions were performed between MHLS and the total number of leaf and hood-like leaf primordia, and between MHLS and the total number of leaves and leaf primordia, respectively and separately for each replication.

Dissections of seedlings ended not necessarily at the same MHLS and stem apical development stages among treatments. Scatter plots of the number of leaf primordia versus the MHLS indicated a bilinear relationship between the two variables in two year × seeding dates × cultivar combinations. Piecewise regression analyses (Ryan and Porth, 2007) returned estimated break points of the bilinear relationships and data past the break points were omitted from the simple linear regressions conducted for the leaf primordium initiation rate estimates.

Estimates of the MHLS at the floral initiation ($MHLS_{FI}$) were obtained from piecewise regression analyses (Ryan and Porth, 2007) between the floral primordia number present at the stem apex and the MHLS. Means of previously mentioned explanatory and response variables were obtained from the six plants replication^{-1} and pooled for the three or four replications block^{-1} (field experiment). The application of a nonparametric smooth to the data indicated an approximate break point. Separate simple linear regression analyses were conducted for the data points before and after that break point, which generated starting values for the PROC NONLINEAR of SAS v9.4 (SAS Institute, 2013). Piecewise regression parameters were obtained and the error variance value was compared to those obtained by following the same procedure for at least one more potential break point value. The parameters derived from that break point value which returned the lowest error variance were selected. At the end, the piecewise model error variance was compared to that of linear and power models and in most cases the segmented regression model returned the lowest error variance.

While determining the Haun stage at floral initiation (HS_{FI}) of the field-grown seedlings would provide evidence of a potential vernalization requirement, the dissections of the controlled-environment-grown seedlings could facilitate the separation of the potentially cofounding effects of temperature and long photoperiod on that response variable.

Estimates of the floral primordium initiation rate were considered as the linear coefficients of the simple linear segments of the bilinear regression models past the break point obtained between MHLS and floral primordia at the stem apex as described earlier, for each plot separately. Estimates of the MHLS at the lowest (last) 1st-order branch primordium appearance ($MHLS_{TS}$, equivalent to the stage of TS formation used for wheat, given that the reproductive commitment at the stem apex of canaryseed plants starts at the top and moves basipetally as in its close relative oat (Landes and Porter, 1990)) were obtained from the bilinear model between MHLS and the floral primordia number after solving the equation for the independent variable (MHLS). The term TS will be used for canaryseed hereafter. The corresponding value of the dependent variable (number of 1st-order branch primordia) used to solve the equation was the average number of 1st-order branches present on a sample of 15-20 panicles per block × cultivar combination (5-6 panicles replication^{-1} for 3 or 4 replications) in 2013 or on a comparable sample of dissected stem apices that had reached the TS stage in 2014. The number of 1st-order panicle branches were counted under a stereoscope after trimming the panicles using small scissors in 2013 or under the stereozoom binocular microscope during the regular seedling dissection events in 2014.

4.2.4.2 Controlled-environment experiment

FLN in the controlled-environment experiments was determined by *in situ* leaf counting on each of the five plants pot^{-1} at or after the flag leaf appearance. Main stem leaves were marked as described above. FLN means were obtained over the five plants pot^{-1} (repetition). Leaf length measurements were conducted at regular intervals of approximately 100-140°Cd on two seedlings replication^{-1} and mean $MHLS_{YL}$ (Haun, 1973) was calculated as described in Chapter 3 for the two seedlings pots^{-1}.

The seedlings for the dissections were obtained from the small pots, which had been previously randomly numbered. One pot at a time was removed from the growth chambers approximately every half or one leaf stage based on the developmental stage of the previously dissected seedlings of each treatment.

The leaf stage of the dissected seedlings and the timing and procedure of the dissections were conducted as described for the field experiment, while means were obtained using the two seedlings pots^{-1}. $MHLS_{FI}$ estimates were obtained as described for the field experiment and means were obtained using the two seedlings small pots^{-1} run^{-1}.

4.2.5 Data analysis

FLN means, estimates of leaf initiation rate, leaf and leaf primordium initiation rate replication^{-1}, $HS_{FI,}$ $MHLS_{TS}$ and floral primordium initiation rate block^{-1} were analyzed using PROC GLIMMIX of SAS v9.4 (SAS Institute, 2013) by year × seeding date and by year × cultivar combinations for the field experiment and by vernalizing temperature × cultivar combinations for the controlled-environment experiment. For the field experiment where means or estimates were obtained replication^{-1}, the block × replication random effect was controlled for heterogeneity of residual variances using the subject option in the random statement of PROC GLIMMIX (Stroup, 2014). When means or estimates were obtained from the pooled data of a whole block, the latter was used as the only random effect for each year × seeding date and year × cultivar combination. For the controlled-environment experiment, FLN means and HS_{FI} estimates were analysed, while, for repetition within each run [repetition (run)] random effect was controlled for heterogeneity of residual variances as described for the field experiment.

To compare and separate the means within each fixed effect, the LSMEANS statement of the GLIMMIX procedure was used to produce t-type tests accompanied by the 'adjust=Tukey' option and pdmix800 (Saxton, 1998). To improve error normality, potential mean outliers were removed before data were subjected to analyses as long as the studentized residual value was higher than 3.0, based on the model for the analysis of the SD effect within the year × cultivar combinations (field experiment) and based on the model for the analysis of the vernalizing duration effect within each temperature × cultivar combination (controlled-environment experiment).

In the analyses of the data from the year × seeding date combinations, means within a year and a SD were subjected to appropriate t-tests and significance was determined at the 5% level. MHLS means repetition^{-1} at regular intervals were subjected to simple linear regressions versus the thermal time from the onset of the vernalizing treatments to obtain an average phyllochron repetition^{-1} as the inverse of the coefficient of the linear component of the model (controlled-environment experiment). Calculation of thermal time for the controlled-environment experiment was conducted based on air temperature. Base temperature was considered 0°C.

4.3 Results

4.3.1 Field experiment

The average (from seeding to near terminal spikelet stage) recorded air temperature for the early, late and very late seeding dates was 13.8, 16.3 and 17.4°C in 2013 and 11.6, 14.9 and 18.1°C in 2014, respectively (Figure 4.1). If considering the temperature up to the first floral initiation for the fastest canaryseed cultivar, the corresponding temperature values are 13.4, 14.7 and 17.4 in 2013 and 11.9, 13.1 and 18.0 in 2014, respectively. The maximum daylength difference within or among SDs was approximately 75 min (Figure 4.1).

Both canaryseed cultivars had significantly higher FLNs on the main stem with late and/or very late compared to early SDs (Table 4.1). The pattern of the differences across SDs differed between the two cultivars. CDC Bastia had the highest FLN when seeded very late in both years and differences between the early and late seeding were smaller compared to the difference between the earliest and latest SD. For Keet, the differences between the late and very late SDs were small and statistically non-significant.

Simple linear regressions between the MHLS and the sum of leaves and hood-like leaf primordium were significant for every single replication block^{-1} in all year × seeding date × cultivar combinations (P<0.05, but in most cases P<0.01, Adj-r^2≥0.85 and mean Adj-r^2=0.96, n=5 to 9) (Figure 4.2). Similarly, the simple linear regressions between the MHLS and the sum of leaves and leaf primordia were significant for every single replication block^{-1} in all year × seeding date × cultivar combinations (P<0.05 but in most cases P<0.001, Adj-r^2≥0.88 and mean Adj-r^2=0.98, n=5 to 7) (Figure 4.3).

The rate of appearance of elongated leaf and leaf primordium was not significantly different among SDs within each year for CDC Bastia. The largest numerical differences observed among SDs within a year for CDC Bastia were 0.11 and 0.06, in 2013 and 2014, respectively. In contrast to the elongated leaf and leaf primordium appearance rate response of CDC Bastia, the cultivar Keet had significantly different values among the three SDs in both years (Table 4.2). The largest numerical differences present among SDs within a year for Keet were 0.25 and 0.23, in 2013 and 2014, respectively. CDC Bastia had a significantly higher elongated leaf and leaf primordium appearance rate than Keet with late SDs in both years.

In general, both cultivars had significantly lower leaf primordium initiation rate values for the late and/or very late compared to the early SDs in both years (Figure 4.3). CDC Bastia had significantly higher leaf primordium initiation rate values than Keet in five out of six year × SD combinations (Table 4.2).

Scatter plots of the floral primordia number initiated at the stem apex versus the MHLS of the seedlings indicated differences in the $MHLS_{FI}$ among SDs within a year for both cultivars and differences between the cultivars in their $MHLS_{FI}$ within SDs (Figure 4.4). Indeed, both canaryseed cultivars initiated their first floral primordium at MHLSs, which were either significantly ($P < 0.05$) or nearly significantly ($P < 0.1$) different among the SDs within each year (Table 4.3). In general, both cultivars in both years initiated their first floral primordium at a later leaf stage when seeded late and/or very late compared to early SD.

The differences in the $MHLS_{FI}$ between cultivars within the SDs and years were similar to those described for the responses in the FLN. Mainly numerical and non-significant differences were observed for the early and very late SDs. These differences were smaller than those observed for the late-seeded crops, when $MHLS_{FI}$ of Keet was significantly later than that shown by CDC Bastia. Like the $MHLS_{FI}$ response of the cultivars, the $MHLS_{TS}$ was either numerically or significantly higher for late and/or very late compared to early SDs (Table 4.3). $MHLS_{TS}$ of Keet was mainly non-significantly higher, than that shown by CDC Bastia except with the late SDs that differences were either significant ($P < 0.05$) or nearly significant ($P < 0.1$). The floral primordium initiation rate responses of the cultivars across SDs within years was similar to their $MHLS_{FI}$ and $MHLS_{TS}$ responses but less defined for the two later SDs (Table 4.3). In general, the floral primordium initiation rate was reduced for the two later SDs compared to early dates and higher overall for CDC Bastia.

For the plant development at or near the stem apex, no relationship was found between the FLN and elongated leaf primordium appearance rate, but FLN was significantly ($P < 0.0001$) and negatively linearly associated with the leaf and leaf primordium initiation rate (Figure 4.5-B). In contrast, both $MHLS_{FI}$ and $MHLS_{TS}$ were significantly ($P < 0.0001$) and positively linearly associated with the FLN (Figure 4.5-C and D, respectively). Consequently, as floral primordium initiation rate is derived from the latter two response variables, it was also similarly related to FLN but the relationship was weaker (Figure 4.5-E).

Table 4.1. Final leaf number (FLN) on main stem for two canaryseed cultivars seeded on three dates in 2013 and 2014.

Cultivar	Stat.An.[1]	2013			Stat. An. SEM[4]	Sign.	2014			Stat. An. SEM	Sign.
		Early	Late	V.Late[5]			Early	Late	V.Late		
		FLN									
Bastia		8.4	**10.3**	**12.6***	0.14	***[4]	8.6	9.2	**11.1***	0.22	***
	s.e.[2]	0.09	0.13	0.19			0.13	0.12	0.26		
Keet		9.4	**12.7**	**13.0**	0.16	***	10.0	**12.0**	**12.6**	0.23	***
	s.e.	0.12	0.15	0.20			0.20	0.20	0.23		
	Sign.[3]	***	***	ns			***	***	**		

[1] Statistical Analysis; [2] Standard Error; [3] Statistical Significance; [4] Standard Error of Mean; [5]Very Late; Cultivar means within a year × seeding date combination were compared by by t-tests. Means in bold differ significantly from the early seeding date mean within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a year×cultivar combination. Mean separations were conducted by Tukey's tests. [5]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.

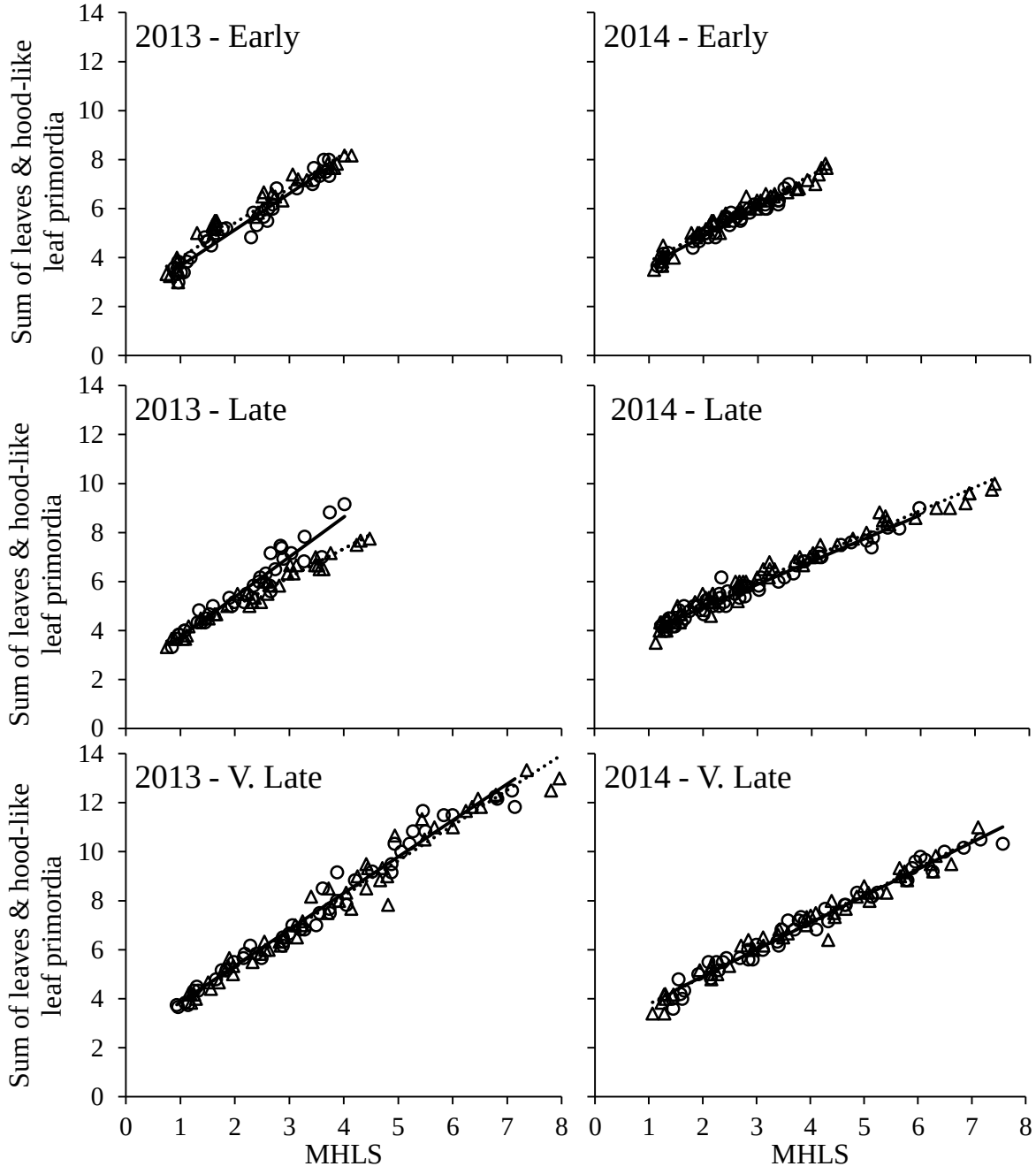

Figure 4.2. Sum of leaves and hood-like leaf primordia versus the modified Haun leaf stage (MHLS) for the canaryseed cultivars CDC Bastia (circles-solid line) and Keet (triangles-dotted line) seeded on three dates in 2013 and 2014. Each data point represents the average of six plants replication^{-1} block^{-1} harvest^{-1}. The slope of the fitted line represents the elongated leaf primordium appearance rate unfolded leaf^{-1} at the stem apex. Statistical analysis is presented on table 4.2.

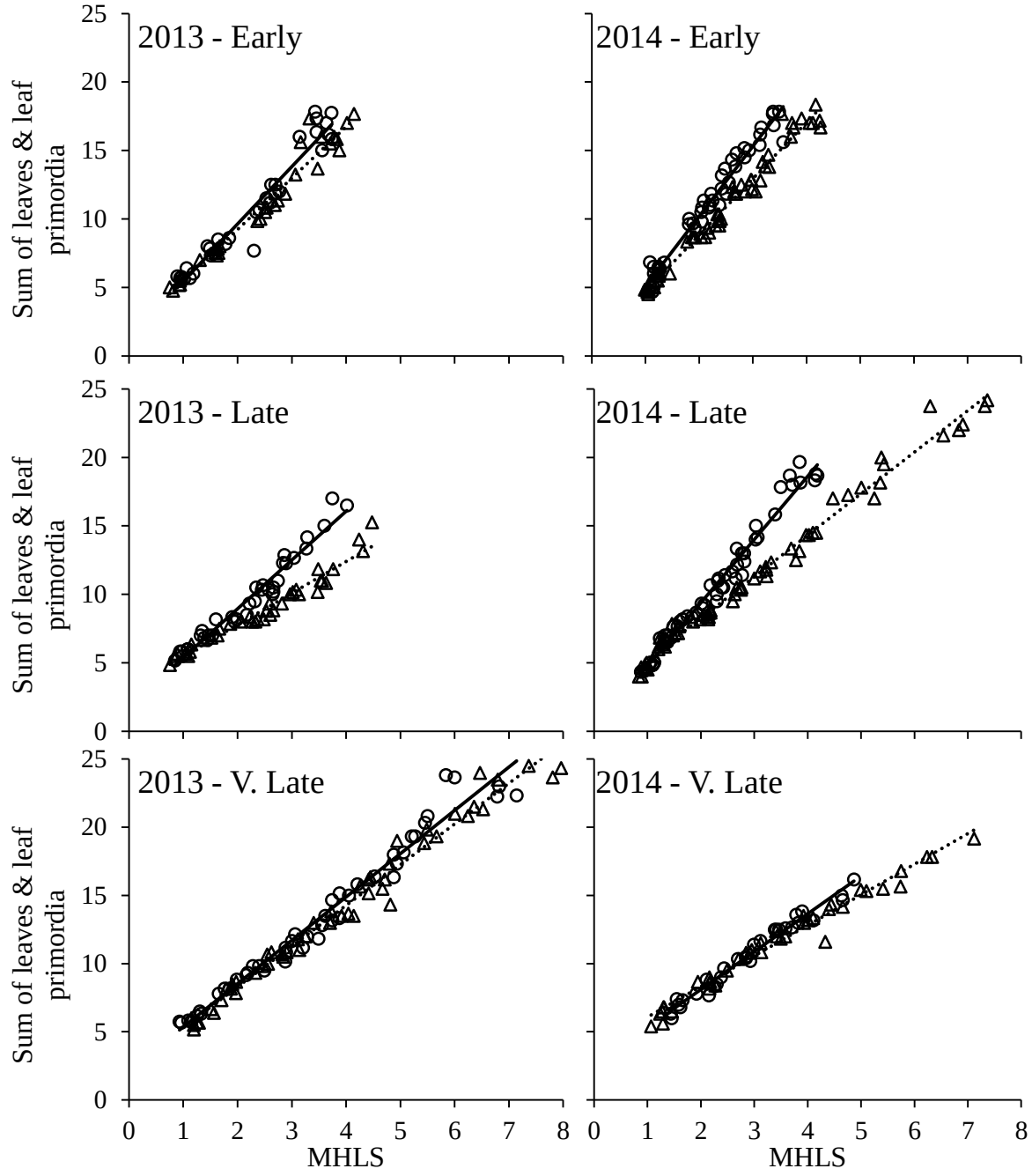

Figure 4.3. Sum of leaves and leaf primordia versus the modified Haun leaf stage (MHLS) for the canaryseed cultivars CDC Bastia (circles-solid line) and Keet (triangles-dotted line) seeded on three dates in 2013 and 2014. Each data point represents the average of six plants replication^{-1} block^{-1} harvest^{-1}. The slope of the fitted line represents the leaf and leaf primordium initiation rate unfolded leaf^{-1} at the stem apex. Statistical analysis is presented on table 4.2.

Table 4.2. Elongated leaf primordium appearance rate and leaf and leaf primordium initiation rate unfolded leaf [1] at the enclosed main stem apex for two canaryseed cultivars seeded on three dates in 2013 and 2014.

Cultivar	Stat.An.[1]				Stat. An.					Stat. An.	
					SEM[4]	Sign.				SEM	Sign.
		2013					2014				
		Early	Late	V.Late[5]			Early	Late	V.Late		
		Elongated leaf primordium apprarance rate									
Bastia	s.e.[2]	1.47 (0.065)	1.58 (0.108)	1.50 (0.032)	0.078	ns[5]	1.03 (0.075)	1.02 (0.025)	1.09 (0.037)	0.059	ns
Keet	s.e.	1.39 (0.030)	**1.20** (0.044)	1.45* (0.027)	0.034	***	1.18 (0.026)	**0.95** (0.019)	1.10* (0.029)	0.027	***
	Sign.[3]	ns	**	ns			+	*	ns		
		Leaf and leaf primordium initiation rate									
Bastia	s.e.	4.29 (0.180)	**3.50** (0.120)	**3.13** (0.147)	0.168	***	5.34 (0.086)	**4.67** (0.104)	**2.84*** (0.125)	0.134	***
Keet	s.e.	3.66 (0.127)	**2.28** (0.226)	**3.02*** (0.085)	0.116	***	4.15 (0.077)	**3.06** (0.075)	**2.33*** (0.111)	0.109	***
	Sign.	*	***	ns			***	***	*		

[1] Statistical Analysis; [2] Standard Error; [3] Statistical Significance; [4] Standard Error of Mean; [5]Very Late; Cultivar means within a year × seeding date combination were compared by by t-tests. Means in bold differ significantly from the early seeding date mean within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a year×cultivar combination. Mean separations were conducted by Tukey's tests. [5]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.

Table 4.3. Modified Haun leaf stage at floral initiation ($MHLS_{FI}$) and at terminal spikelet ($MHLS_{TS}$) and the floral primordium initiation rate for two canaryseed cultivars seeded on three dates in 2013 and 2014.

Cultivar	Stat.An.[1]				Stat. An.					Stat. An.	
					SEM[4]	Sign.				SEM	Sign.
		2013					2014				
		Early	Late	V.Late			Early	Late	V.Late		
		$MHLS_{FI}$									
Bastia	s.e.[2]	2.44 (0.083)	2.69 (0.005)	3.66 (0.325)	0.19	+[6]	2.11 (0.071)	**2.53** (0.036)	**3.61** (0.330)	0.20	+[7]
Keet	s.e.	2.34 (0.022)	**3.52** (0.018)	**4.11*** (0.240)	0.14	*	2.43 (0.008)	3.73 (0.133)	4.42 (0.430)	0.26	+[8]
	Sign.[3]	ns[5]	***	ns			*	*	ns		
		$MHLS_{TS}$									
Bastia	s.e.	4.10 (0.115)	7.24 (0.765)	7.11 (0.740)	0.618	+[9]	3.74 (0.240)	4.49 (0.165)	6.92 (0.665)	0.419	+[10]
Keet	s.e.	5.38 (0.620)	**9.52** (0.015)	8.23 (0.240)	0.384	*	4.89 (0.375)	7.71 (0.175)	**7.97** (0.805)	0.523	*
		ns	+	ns			ns	**	ns		
		Floral primordium initiation rate									
Bastia	s.e.	5.93 (0.087)	**2.65** (0.447)	**3.53*** (0.482)	0.383	*	6.05 (1.114)	5.67 (0.505)	3.74 (0.400)	0.743	ns
Keet	s.e.	3.20 (0.447)	2.16 (0.000)	2.79 (0.076)	0.374	ns	3.69 (0.588)	3.04 (2.744)	3.36 (0.037)	0.381	ns
	Sign.	+	ns	ns			ns	*	ns		

1 Statistical Analysis; 2 Standard Error; 3 Statistical Significance; 4 Standard Error of Mean; 5Very Late; Cultivar means within a year × seeding date combination were compared by by t-tests. Means in bold differ significantly from the early seeding date mean within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a year×cultivar combination. Mean separations were conducted by Tukey's tests. 5ns, +, *, ** and *** used to denote that the statistical significance within

a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. [6] $P = 0.0825$, [7] $P = 0.0560$, [8] $P = 0.0618$, [9] $P = 0.0736$, [10] $P = 0.0599$

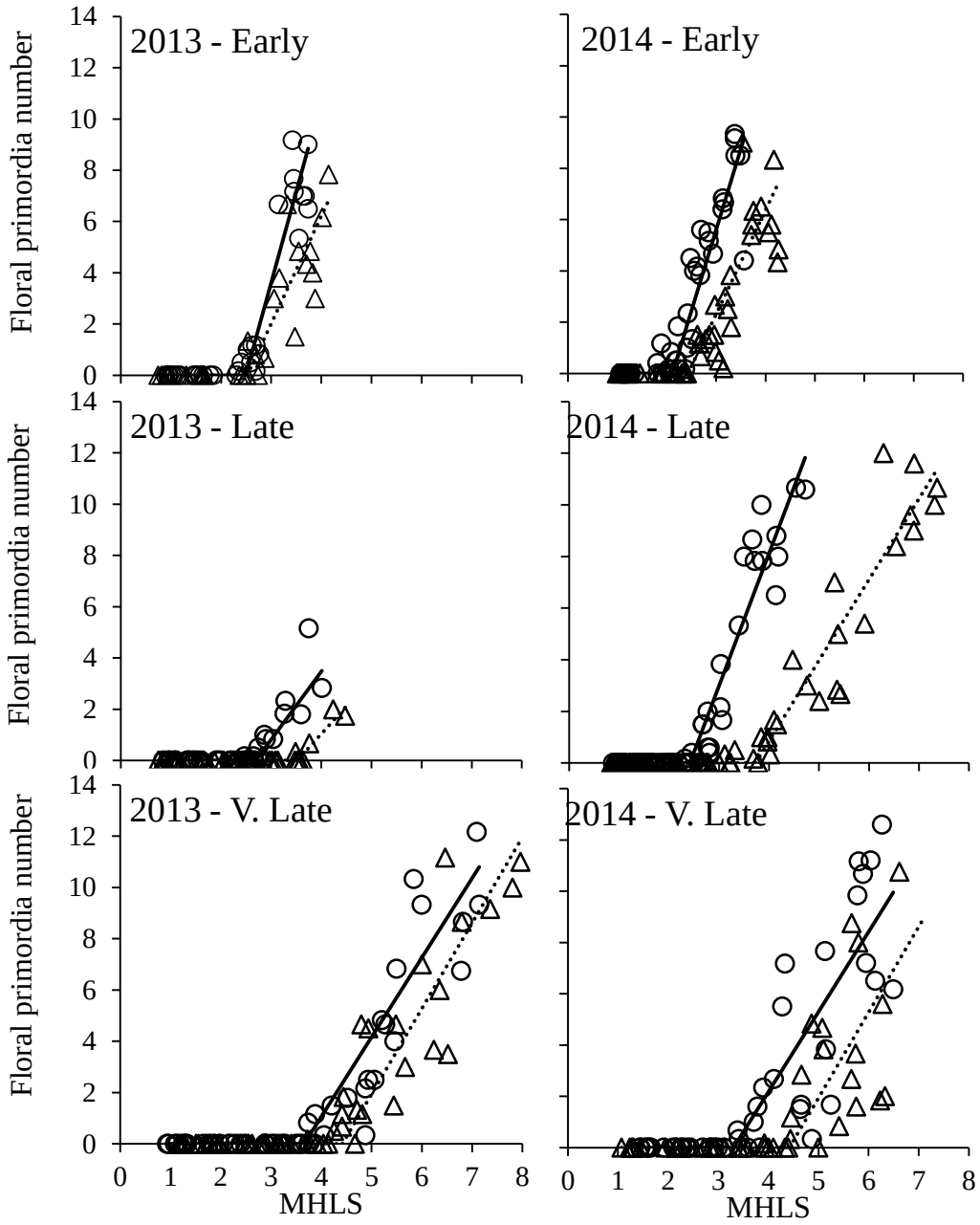

Figure 4.4. Floral primordia number versus the Modified Haun leaf stage (MHLS) for the canaryseed cultivars CDC Bastia (circles-solid line) and Keet (triangles-dotted line) seeded on three dates in 2013 and 2014. Each data point represents the average of six plants replication^{-1} block^{-1} harvest^{-1}. The lines were fitted by piecewise regression using the average break point from the statistical analysis presented on table 4.3. The break point and the slope of the fitted line past the break point represent the MHLS at the first floral primordium initiation and the floral primordium initiation rate unfolded leaf^{-1} at the stem apex, respectively.

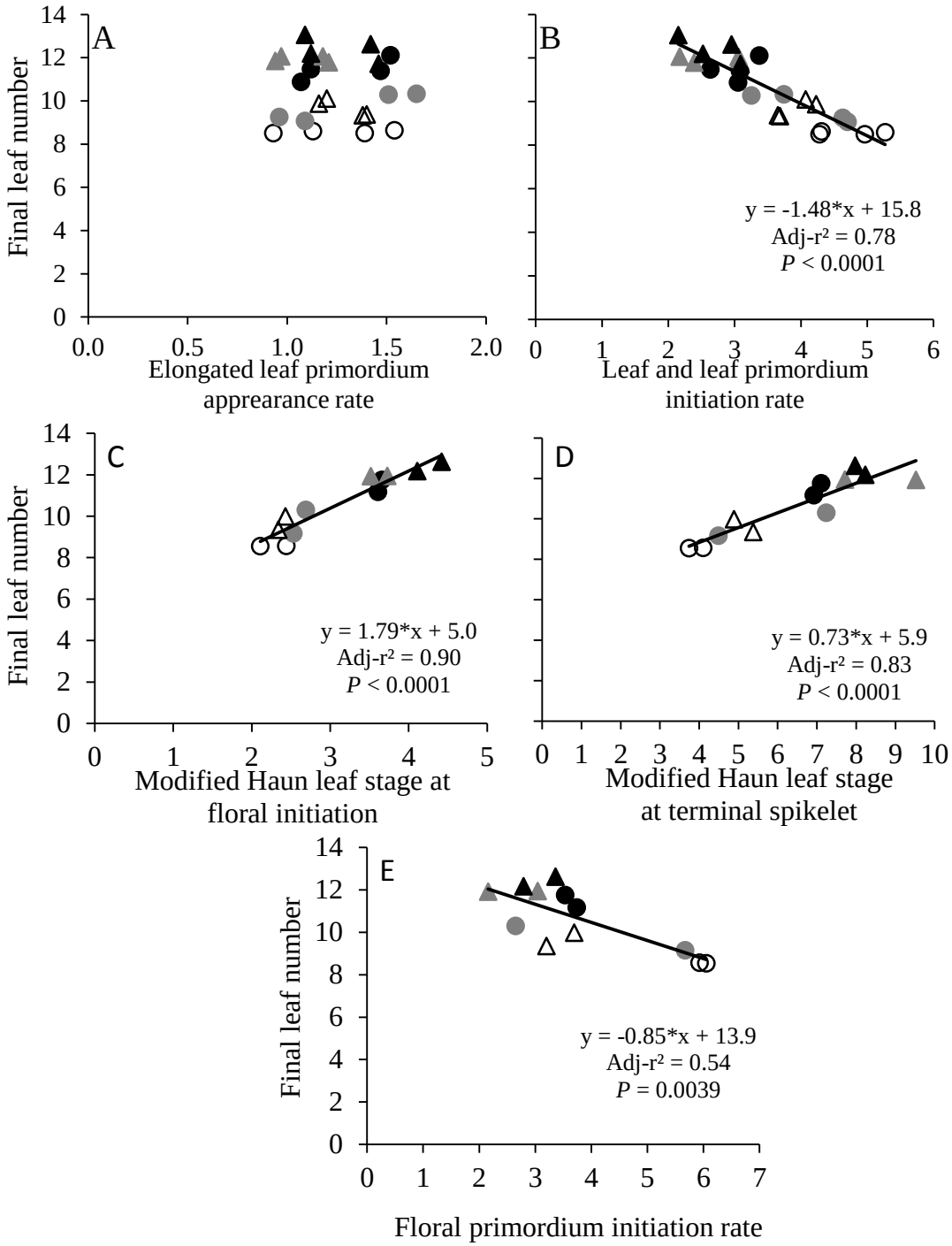

Figure 4.5. Final leaf number versus the elongated leaf primordium appearance rate (A), the leaf and leaf primordium initiation rate (B), the modified Haun leaf stage at floral initiation (C) the modified Haun leaf stage at the terminal spikelet (D) and the floral primordium initiation rate (E) for the canaryseed cultivar CDC Bastia (circles) and Keet (triangles) seeded early (open symbols), late (grey-closed symbols), and very late (black-closed symbols) in 2013 and 2014.

4.3.2 Controlled-environment experiment

For the average, over the three vernalizing temperatures and the five durations, the FLN of wheat and oat cultivars was 8.29(s.d. = 0.25) and 8.83(s.d. = 0.24), respectively. Canaryseed cultivars CDC Bastia and Keet, in turn, had a higher average FLN of 11.16(s.d. = 1.09) and 16.28(s.d. = 1.84), respectively (Figure 4.7 and Appendix 1). Both wheat and oat cultivars had significantly lower FLNs with prolonged exposure to 5°C and 10°C compared to shorter vernalizing durations, but when exposed to 15°C, FLN means of different durations were non-significantly different (Figure 4.7). The maximum differences in the FLN of wheat and oat due to exposure to different vernalizing durations were as small as 0.5 and 0.7 leaves, respectively. Both canaryseed cultivars, in turn, had significantly lower FLN with prolonged exposure to 10°C compared to the control treatment of up to 2.3 and 4.0 leaves, respectively. The wheat and oat cultivars had reduced FLNs at least up to the longer vernalizing duration when exposed to 5°C. However, at 10°C, the lowest FLN was already reached with a 14-day exposure and this was the case with both canaryseed cultivars as well. Keet always had higher FLN means compared to CDC Bastia across the temperature × vernalizing duration combinations. The differences ranged from 3.0 (ie, 10°C – 21d) to 7.6 (ie, 15°C – 14d) leaves, while the average difference, among durations, was higher at 15°C (6 leaves) compared to 5°C (5.1 leaves) and 10°C (4.5 leaves).

Scatter plots of the floral primordia number initiated at the stem apex versus the MHLS of the seedlings indicated relatively larger differences in $MHLS_{FI}$ among vernalizing temperatures and durations for the canaryseed cultivars compared to wheat and oat (Figure 3.6). $MHLS_{FI}$ data at 5 and 10°C vernalizing temperatures for Keet is not complete because of the initiation of floral primordia at a late MHLS when no seedlings were left for dissection and therefore the $MHLS_{FI}$ could not be morphologically accurately quantified (Figure 4.6).

The wheat and oat cultivar initiated their first floral primordium at the stem apex at an average $MHLS_{FI}$ of 3.1(s.d. = 0.31) and 2.88(s.d. = 0.20), respectively. CDC Bastia had an average $MHLS_{FI}$ of 3.31(s.d. = 0.64) while that of Keet at 10°C was 4.95(s.d. = 0.65) (Table 4.4). In general, wheat and oat had relatively small, mostly non-significant differences in $MHLS_{FI}$ among durations within each vernalizing temperature. However, when seedlings were exposed to 15°C for 21d, they had a significantly ($P < 0.05$) delayed floral primordia initiation compared to those exposed to the same temperature for shorter durations. When exposed to 10°C for seven or 14d, both canaryseed cultivars initiated floral primordia at significantly significantly ($P < 0.05$), or nearly significantly ($P < 0.1$), earlier MHLSs compared to shorter and/or shorter vernalizing durations.

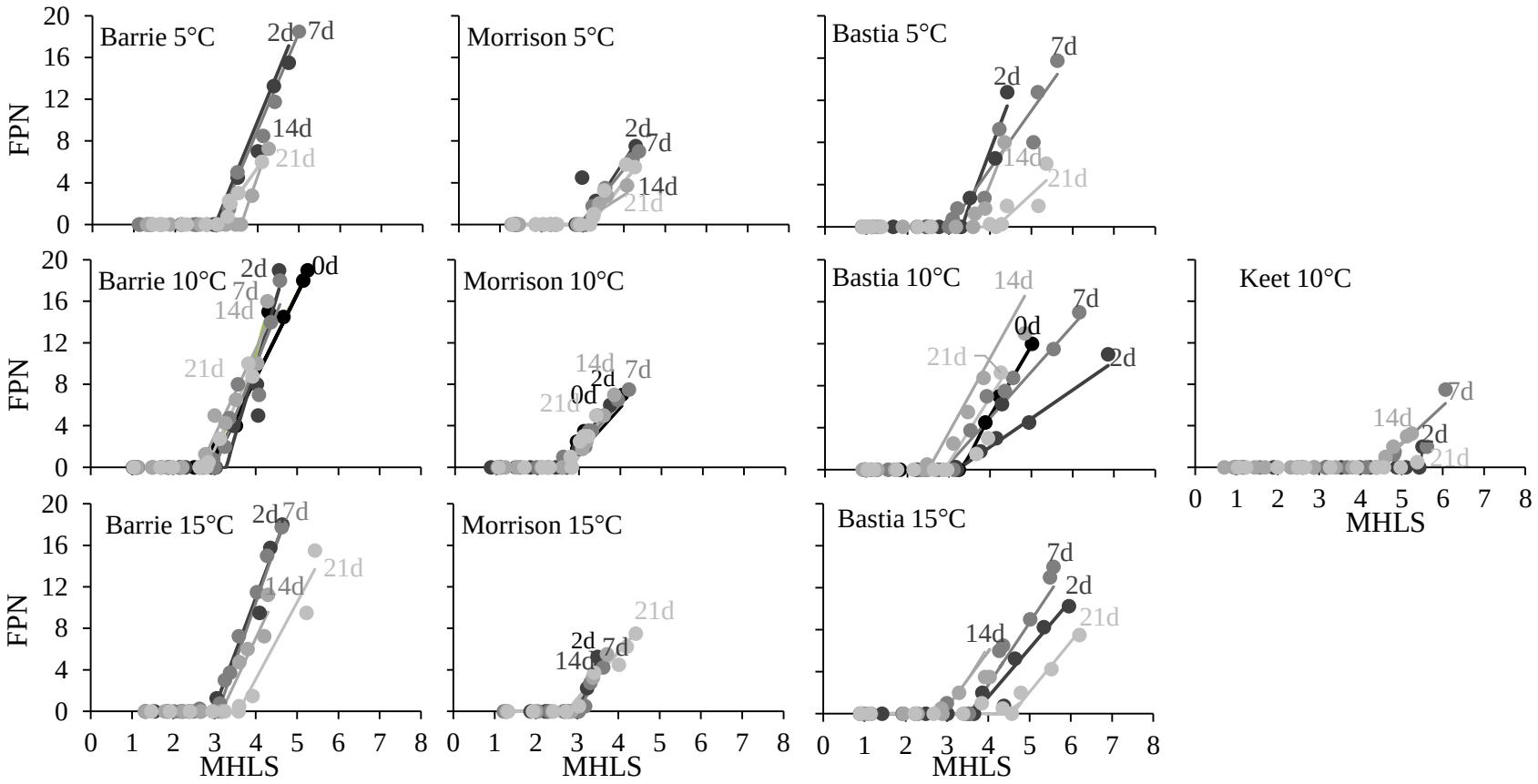

Figure 4.6. Floral primordia number (FPN) versus the modified Haun leaf stage (MHLS) for two canaryseed, one wheat and one oat cultivar exposed to three vernalizing temperatures for five durations (d). Data points are the means of two replications and two plants replication^{-1}. The lines were fitted by piecewise regression using the average break point of the two replications whose statistical analysis is presented on table 4.4 The break point and the slope of the fitted line past the break point represent the MHLS at the first floral primordium initiation and the floral primordium initiation rate unfolded leaf^{-1} at the stem apex, respectively.

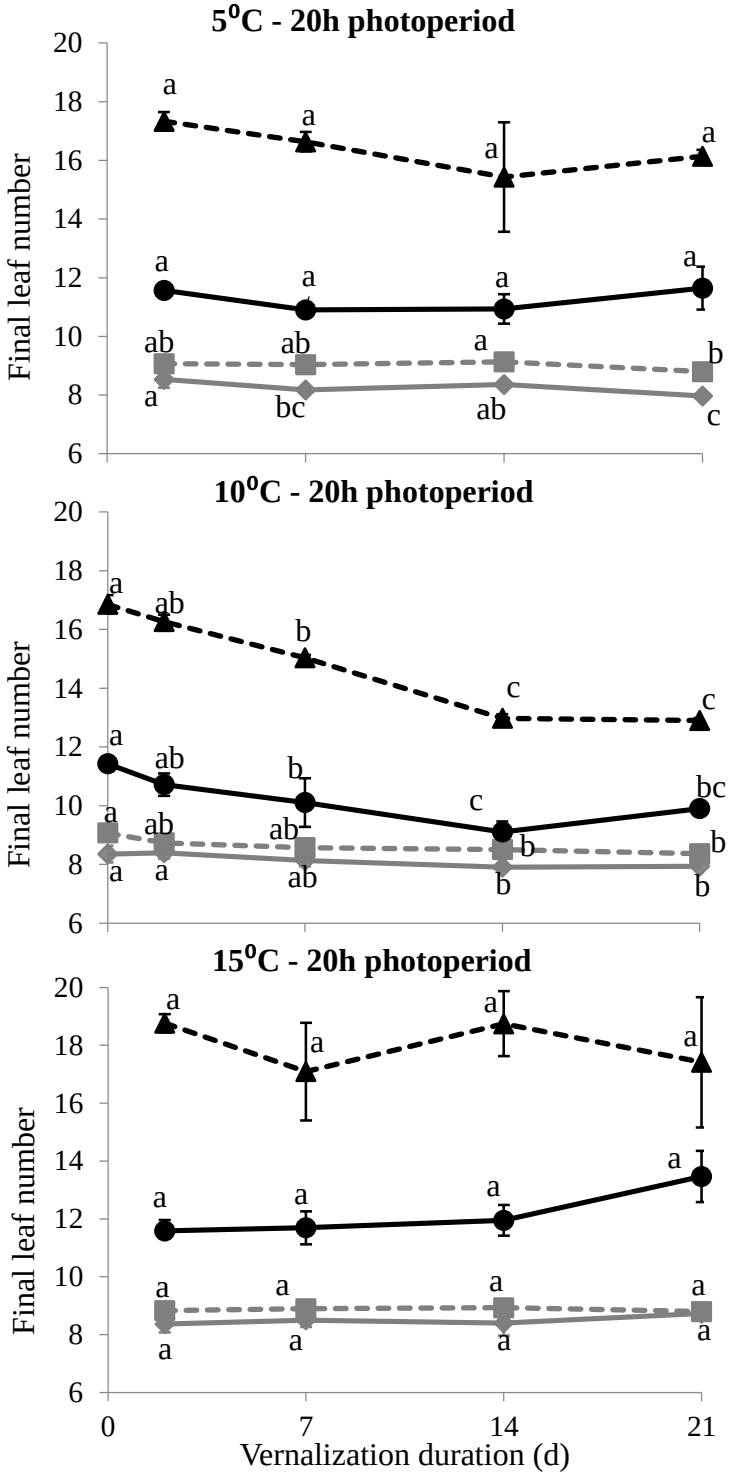

Figure 4.7. Final leaf number for two canaryseed (CDC Bastia, black-solid line; Keet, black-dashed line), one spring wheat (AC Barrie, grey-solid line), and one oat cultivar (CDC Morrisson, grey-dashed line) vernalized at three air temperatures (5, 10 and 15°C) for five durations. Vertical bars (where larger than treatment symbols) represent standard error. Means within a cultivar and vernalizing temperature followed by the same letters do not differ significantly at the 5% level. Means separation conducted by Tukey test.

Table 4.4. Modified Haun leaf stage at floral initiation ($MHLS_{FI}$) for two canaryseed, one wheat, and one oat cultivars vernalized at three temperatures for five durations.

Cultivar	Vernalizing duration (d)					Stat. An.	
						SEM	Sign.
	0	2	7	14	21		
	5°C - 20h photoperiod						
Bastia	-	3.57[a]	3.00[a]	3.52[a]	4.34[a]	0.629	ns
Keet	-	≥7.28[1]	≥7.44	≥4.37	>4.80	-	-
Barrie	-	3.09[a]	3.03[a]	3.59[a]	3.00[a]	0.105	+
Morrison	-	2.99[a]	2.92[a]	2.88[a]	3.18[a]	0.087	ns
	10°C - 20h photoperiod						
Bastia	3.23[a]	3.20[a]	2.88[ab]	2.50[b]	2.88[ab]	0.143	*
Keet	5.88[a]	5.43[a]	4.40[a]	4.38[a]	5.09[a]	0.310	+
Barrie	2.93[a]	3.27[a]	3.00[a]	2.64[a]	2.80[a]	0.142	ns
Morrison	2.81[a]	2.70[a]	2.59[a]	2.87[a]	2.82[a]	0.181	ns
	15°C - 20h photoperiod						
Bastia	-	4.13[ab]	3.53[ab]	2.89[b]	4.57[a]	0.232	*
Keet	-	≥6.34	≥5.63	>4.28	>5.73	-	-
Barrie	-	2.97[b]	3.09[b]	3.17[b]	3.71[a]	0.087	*
Morrison	-	3.01[a]	3.04[a]	2.86[a]	2.73[a]	0.161	ns

[1]: All values of $MHLS_{FI}$ for the canaryseed cultivar Keet at 5 and 15°C were omitted from the statistical analyses.
[2]: Means within a cultivar and vernalizing duration followed by the same superscript letters do not differ significantly at the 5% level. Means separation conducted by Tukey's test.

A significant ($P < 0.0001$) positive linear relationship between FLN and $MHLS_{FI}$ was observed when considering all the experimental data obtained from the controlled-environment experiment (Figure 4.8-A). In addition, the relationship seems to hold when using the data from both the field and the controlled-environment experiments (Figure 4.8-B).

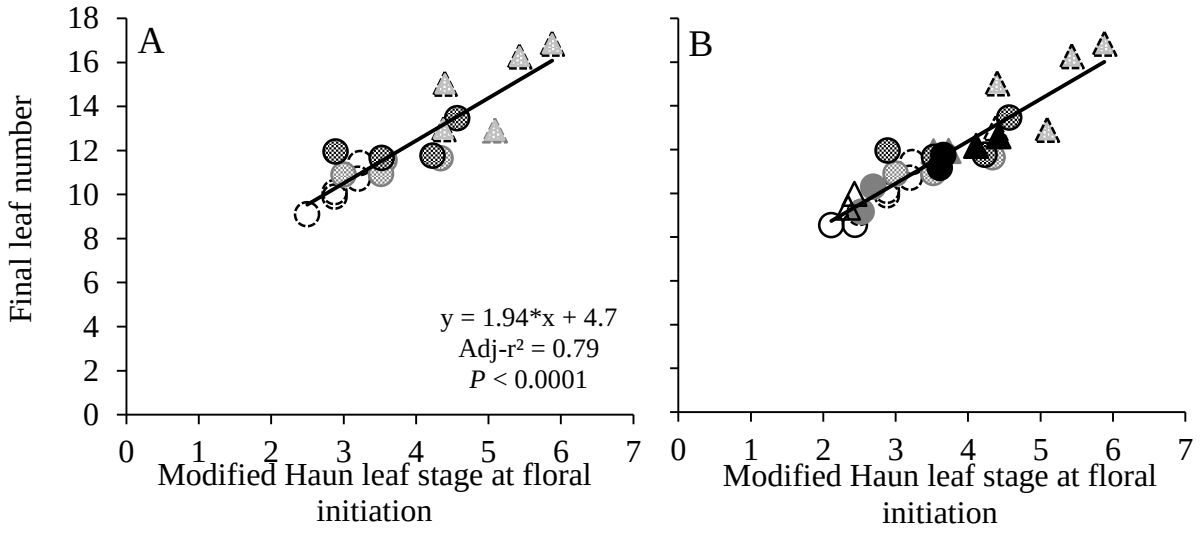

Figure 4.8. Final leaf number (FLN) versus the modified Han leaf stage at floral initiation ($MHLS_{FI}$) for the canaryseed cultivar CDC Bastia (circles) and Keet (triangles) when exposed to 5°C (open symbols – dotted line), 10°C (grey-patterned closed symbols) and 15°C (black-patterned closed symbols) vernalizing temperatures and five different durations (A) and FLN versus the $MHLS_{FI}$ for the canaryseed cultivars CDC Bastia and Keet when grown at the field experiment and in the controlled-environment experiment described in section 3.3 (B). For symbols, patterns and colors in figure B see figure 4.8-A and figure 4.5.

4.3.3 Short experiment in a controlled-environment

Germinated wheat and oat seeds or young seedlings (approximately one leaf unfolded) that were exposed to an 8h photoperiod at 10°C for 14d showed differences in mean FLNs of up to 0.5 leaves (Table 4.5). Half a leaf was also the maximum FLN mean difference for the wheat and oat cultivars exposed to those vernalizing conditions, but to slightly different post-vernalizing growth conditions. In contrast to the wheat and oat cultivars, CDC Bastia and Keet had maximum FLN mean differences of 3.0 and 2.5 leaves, respectively, when comparing the growth stage at the onset of the vernalizing treatment, and differences of 2.9 and 3.1 leaves, respectively, when comparing the different post-vernalizing treatments (Table 4.5).

In general, wheat and oat cultivars had very similar FLN means between the two different growth stages at the onset of the vernalizing treatment and between the two different post-vernalizing growth conditions. On the other hand, both canaryseed cultivars had higher FLN means when young seedlings were exposed to vernalizing conditions, compared to the germinated planted seeds, and under the 17h, compared to the 20h, photoperiod. Furthermore, Keet showed the lowest FLN of all the controlled-environment treatments (9.0 leaves) when germinated seeds were exposed to vernalizing conditions and the seedlings were grown under a 17h photoperiod thereafter.

Table 4.5. Final leaf number on plants from two canaryseed, one spring wheat and one oat cultivars which were exposed to 8h photoperiod at 10°C for 14d either as young seedlings or germinated planted seeds.

Growth stage at the onset of vernalizing treatment	Cultivar	Final leaf number	
		Post-vernalizing growth conditions	
		20h photoperiod - 20°C	17h photoperiod - 23/15°C [1]
Seedling	CDC Bastia	12.3 (1.00)[2]	10.4 (0.38)
	Keet	14.4 (0.08)	11.5 (0.50)
	AC Barrie	9.0 (0.00)	9.5 (0.00)
	CDC Morrison	8.9 (0.10)	9.1 (0.13)
Germinated planted seed	CDC Bastia	9.3 (0.10)	8.7 (0.15)
	Keet	12.1 (0.45)	9.0 (0.40)
	AC Barrie	8.6 (0.40)	9.0 (0.23)
	CDC Morrison	9.4 (0.38)	9.1 (0.13)

[1] Day/Night
[2] Numbers in brackets represent standard error

4.4 Discussion

Temperature and photoperiod are the most critical factors determining temperate cereal phenological development (Baker and Gallagher, 1983a and b; Cao and Moss, 1989a and b; Sonego, 2000). Temperate cereal responses to vernalization, photoperiod and their interaction are phenotypically expressed with changes in the FLN produced on the main stem of the plants

(Brooking et al., 1995; Mahfoozi et al., 2001a and b; Brooking and Jamieson, 2002). This study investigated morphological responses of canaryseed cultivars to different air temperatures. The main objective was to document potential FLN response of canaryseed cultivars to different SDs by investigating its relation to potential low-temperature vernalization requirement or to the leaf-development pattern of the cultivars. To meet the main objective, field and controlled-environment experiments were conducted.

4.4.1 Field experiment

The average recorded air temperature was increased with delayed seeding in both years. In addition, both canaryseed cultivars exhibited higher FLNs with delayed seeding.

Given the numerical differences in elongated leaf primordium appearance rate values among seeding dates within a year for CDC Bastia and considering the FLN, differences in the FLNs between treatments related to elongated leaf primordium appearance rate could be no higher than approximately one leaf in 2013 and 0.66 of a leaf in 2014. However, maximum FLN differences among SDs within a year for CDC Bastia were three-fold (3.2 leaves) and four-fold (2.66 leaves) higher in 2013 and 2014, respectively. For Keet, the differences in the FLN between treatments related to elongated leaf primordium appearance rate could be up to approximately 3.25 leaves in 2013 (ie, higher FLNs for the very late compared to late SD) and 2.30 leaves in 2014 (ie, higher FLN for the early compared to late SDs). However, neither of those expected FLN differences, based on the elongated leaf primordium appearance rates, were exhibited. The two later SDs in 2013 did differ in FLN. In 2014, however, the FLN differences between the early and late SDs were numerically similar to what would have been expected due to elongated leaf primordium appearance rate differences but in the opposite direction (ie, the late SD had higher FLN compared to the early SD). In other words, for CDC Bastia, although the late and/or very late SDs had slight differences in elongated leaf primordium appearance rate values compared to the early SDs, those differences were not sufficient to explain the corresponding differences in the FLNs. Differences in the the elongated leaf primordium appearance rates of Keet did not correspond to measured differences in the FLNs. Thus, the hypothesis that the elongated leaf primordium appearance rate responses of the canaryseed cultivars to higher air temperatures, related to delayed seeding, could explain potential differences in the FLN among SDs was disproved.

The hypothesis that the increased FLN for canaryseed with delayed seeding is related to higher recorded air temperature and not to the leaf-development pattern of canaryseed is plausible for the following reasons:

The $MHLS_{FI}$ and $MHLS_{TS}$ of both canaryseed cultivars increased with delayed seeding. Such a response agrees with the findings on the vernalization and photoperiod responses of wheat, as determined morphologically at its stem apex (Brooking, 1996; Robertson et al., 1996; Brooking and Jamieson, 2002). In addition, both response variables were positively and linearly related to the FLN (Figure 4.5 – C and E), which again is in line with findings for wheat (Jamieson et al., 2007; Brown et al., 2013) and oat (Sonego et al., 2000).

While the $MHLS_{FI}$ and $MHLS_{TS}$ of the field-grown seedlings and their relationship with the FLN provided some evidence of a potential vernalization requirement for the canaryseed cultivars, diurnal air temperature fluctuations and potential differences in soil water (especially with very late seeded crops) and nutrient availability (less likely due to fertilizer application) among SDs might have caused part of the FLN differences among treatments. In addition, the potential interaction between the long photoperiod with temperature during vernalization could be a factor. For instance, in wheat, the vernalization rate, expressed as the change in the FLN per duration of the seedlings exposure to low temperature, is modified under long photoperiod once the temperature is higher than 8°C (Brooking and Jamieson, 2002). While recorded average air temperature during early SDs was higher than 8°C, and nighttime air temperatures near or even lower than that, average air temperature during the later SDs was well above 8°C. If canaryseed cultivars responded to a potential interactive effect of temperature with the long photoperiod, that would be more likely with delayed seeding.

Therefore, the potential cofounding effects of fluctuating air temperature, soil water, nutrient availability and the interactive effects of higher air temperature with long photoperiod on the FLNs, $MHLS_{FI}$ and $MHLS_{TS}$ need to be eliminated to determine the effect of temperature on the potential low-temperature vernalization requirement of canaryseed cultivars.

4.4.2 Controlled-environment experiment

The exposure of young canaryseed seedlings to different temperatures with varying durations resulted in non-significant effects on FLNs and/or $MHLS_{FI}$ at 5°C and 15°C (Figure 4.7 and Table 4.4). At 10°C, however, these effects were significant as both response variables were reduced with the prolonged exposure of the seedlings to that temperature up to a period of 14d. These results indicate that both canaryseed cultivars responded to low-temperature vernalizing treatments under a very long photoperiod. The 5°C and 15°C, in contrast, were less effective in lowering either the FLN or the $MHLS_{FI}$. The responses of the canaryseed cultivars in FLN and $MHLS_{FI}$ to the three air temperature treatments were consistent with previously reported results for wheat vernalization and photoperiod responses. For instance, both

canaryseed cultivars exhibited non-significant reductions in their FLNs with prolonged exposure to 5°C (Figure 4.7). The FLNs for different durations at that temperature was always higher compared to 10°C, the most effective vernalizing treatment in terms of reducing the FLN. Similar results have been reported by Brooking and Jamieson (2002) in spring wheat when young seedlings were exposed to 5 and 8°C under long days. In the current study, the wheat and oat seedlings exhibited similar results after exposure to 5 and 10°C under long days, but the differences between the two temperatures and different durations were smaller than those Brooking and Jamieson (2002) reported for spring wheat isogenic lines.

Given the relationships shown between FLN and $MHLS_{FI}$ in the present study (Figure 4.8), any differences in the FLN response of canaryseed to vernalizing treatments correspond to differences in their $MHLS_{FI}$. When combining the FLN and $MHLS_{FI}$ data from the field and the controlled-environment experiments in the same figure, the relationship between the two variables seems to become even stronger than using the data from the latter experiment only. Such a relationship is consistent with those reported for wheat (Jamieson et al., 2007; Brown et al., 2013) and oat (Sonego et al., 2000).

Keet had a wider range of FLNs compared to CDC Bastia across vernalizing durations at all three temperatures in the controlled-environment experiment (Figure 4.7) and higher FLN means in all treatments in both the field and the controlled-environment experiments (Table 4.1 and Figure 4.7). FLN mean differences were larger under controlled conditions, especially at 15°C. Brooking and Jamieson (2002) reported a wider FLN mean range for a winter wheat isoline compared to a spring wheat isoline across vernalizing durations under long days. The range was wider at 11°C than at 5°C and 8°C. In addition, the reported FLN mean differences between the two wheat isolines were larger at 11°C than at the lower temperature regimes. Considering the highest mean value in the FLNs of Keet in the controlled-environment experiment (ie, 19.6 leaves), Keet exhibited a response to temperature that was similar to that shown by the winter wheat isoline reported by Brooking and Jamieson (2002). In contrast to Keet, CDC Bastia had a narrower range across vernalizing durations at all three temperatures and lower FLN means for all treatments in both the field and the controlled-environment experiments. Considering the relatively low upper values in the FLN means of CDC Bastia in the controlled-environment experiment (ie, 13.5 leaves), it exhibited a low temperature response like that of the spring wheat isoline evaluated by Brooking and Jamieson (2002).

Regardless of the reductions in the FLN of both canaryseed cultivars with the prolonged exposure of the seedlings to 10°C, the lowest FLN of Keet in the controlled-environment

experiment was 12.9 that is 3.5 leaves greater than the lowest FLN in the field experiment. The following could account for that difference:

(1) It has been postulated that most crop species of Mediterranean, or temperate, origin have long day requirements (Summerfield et al. 1997, Thomas and Vince-Prue 1997). Given the center of origin of canaryseed, it is likely a long day plant. Daylengths of 16h or longer are often considered sufficiently long to induce the transition to reproductive development for temperate cereals. Therefore, the difference in daylength between the field and the controlled-environment experiments might have caused minor differences in the FLN of the plants. However, the difference would have been expected to be in the opposite direction of the one observed. Native grass species within or near the Mediterranean region flower in the spring, while the transition from the vegetative to the reproductive phase occurs somewhat earlier. That is, both phenological stages occur under substantially shorter natural daylength than that of both experiments in this study, while the daylength used in the controlled-environment experiment was approximately 3h to 3.5h longer than that in the field experiment. Therefore, a potential requirement for shorter daylength prior to the FLN determination might have caused the differences for the lowest FLN means between the two experiments.

(2) Vernalization in cereals is an active process commencing at seed imbibition. In the field experiment, therefore, the onset of the fulfillment of a potential vernalization requirement for canaryseed could have commenced with seed imbibition. In contrast, in the controlled-environment experiment, young seedlings (at approximately the 1st leaf stage) were exposed to low temperatures. Regardless of the number of leaf primordia already present in the seed embryo, based on the average leaf and leaf primordium initiation rate unfolded leaf^{-1} (Table 4. 3), a seedling at the 1st leaf stage will have already had initiated three or four more leaves and leaf primordia in total, depending on the cultivar, compared to an imbibed seed. Considering that vernalization shortens the duration of leaf primordia initiation by causing the first floral primordium to appear at a younger physiological age (based on the leaf stage), the reproductive commitment that moves basipetally will have to overgrow three or four more leaf primordia, depending on the cultivar, for fully vernalized plants from the two experiments to form an equal FLN. Alternatively, the plants from the controlled-environment experiment will form three or four more leaves. Although this rationale already explains the difference in the lowest FLN between the two experiments for Keet, a third reason, which also supports the current explanation, follows.

(3) According to Wang et al. (1995), for the winter wheat cultivar "Pioneer 2548" with a vernalization requirement, "the minimum vernalization duration required to reach a stage of

vernalization insensitivity decreased as plant age at the onset of vernalization increased." The onset of the fulfillment of Keet potential vernalization requirement in the controlled-environment experiment commenced at a higher plant physiological age, compared to the field experiment, which may have caused the plants to reach vernalization saturation earlier, in terms of duration of exposure to low temperature. However, when plants of different physiological age experience similar vernalizing conditions (ie, early SDs in the field experiment and 10°C-14d treatment in the controlled-environment experiment), they will likely form different FLN as explained in the rationale (2) above.

A short experiment was conducted to provide more evidence regarding the three possible reasons for the difference in the lowest FLN between the two experiments of Keet.

4.4.3 Short experiment in a controlled environment

The difference in the FLN of the canaryseed cultivars between the two different post-vernalizing growth conditions that were previously exposed to short day (8h) vernalizing conditions suggests that, regardless of the physiological age of the plant at the onset of the vernalizing treatment, the 3 h longer photoperiod (ie, from 17h to 20h) increased the FLN of both cultivars (Table 4.5). There is no other documented information on the potential vernalization requirement of canaryseed and therefore the results of this study cannot be compared. However, such a response to post-vernalizing plant growth conditions from a species belonging to the grass family contrasts what Ream et al. (2014) reported on the grass species, brachypodium (*Brachypodium distachyon*). When imbibed seeds of brachypodium were vernalized under an 8h photoperiod for several different periods of time and then exposed to either a 16h or 20h photoperiod, days to flowering, and thus FLN (a strong correlation is reported between the two variables), were reduced under the longer photoperiod, post-vernalizing conditions. Ream et al. (2014) reported that the seedlings vernalized for one to four weeks rarely emerged from the soil by the end of their vernalization period, while seedlings that were vernalized for longer periods had only their coleoptile emerged. Only seedlings from the very long vernalizing treatments had one leaf unfolded. It is not clear, therefore, how seedlings from shorter or longer vernalizing periods sensed and responded to photoperiod. The response of the canaryseed cultivars to the post-vernalizing growth conditions is a topic that requires further investigation.

Of interest is the observation that the exposure of young canaryseed seedlings of both cultivars to 10°C for 14d and an 8h photoperiod followed by exposure to 20°C with a 20h photoperiod resulted in higher FLN and therefore higher $MHLS_{FI}$ (ie, see the regression in

Figure 4.8-A) compared to a 20h photoperiod during the cold exposure. Therefore, a short photoperiod of at least 8h during the vernalizing treatment of the canaryseed seedlings is as or less effective, in reducing the FLN and the $MHLS_{FI}$, than the very long photoperiod of 20h. That would concur with the fact that the germinated planted seeds of both canaryseed cultivars had lower FLNs when vernalized under the short photoperiod compared to the young seedlings in the corresponding treatments. The tip of their emerged first leaf under the short photoperiod enabled them to start sensing the photoperiod sometime during the vernalizing treatment and therefore they were vernalized under the very long photoperiod for fewer days.

4.5 Conclusions

Canaryseed cultivars exhibited different FLNs when grown in the different environments that resulted from different seeding dates. Differences in the rate of elongated leaf primordium appearance among seeding dates were either small or did not correspond to those of the FLN. In contrast, the modified Haun leaf stage at the floral initiation of field-grown seedlings from both canaryseed cultivars correlated with their FLN. Both canaryseed cultivars responded to low (5°C) or relatively low temperature (10°C) vernalizing treatments under the very long photoperiod by reducing the final leaf number on main stem and the modified Haun leaf stage at the floral initiation with exposure of the seedlings for up to 14d. Canaryseed final leaf number appeared sensitive to both physiological age at the onset of vernalizing treatment and the post-vernalization growth conditions.

Transition section between Chapter 4 and Chapter 5

The impact of seeding time on the apical development of canaryseed and whether it is related to the potential low-temperature vernalization requirement of the crop or to its leaf-development pattern was the subject of Chapter 4. A putative low-temperature vernalization requirement of canaryseed was proposed based on evidence from the plant response to contrasting seeding dates and vernalizing treatments. Given the impact of unmet vernalization requirements on the time to anthesis of other small grain temperate cereals, the first objective of the experiments of Chapter 5 is to investigate a determinant of the time to anthesis in cereals, namely leaf appearance or its inverse, the phyllochron, of canaryseed, relative to wheat and oat. The second objective is to investigate the tillering pattern of canaryseed relative to spring wheat and oat, in relation to plant phenology and canopy light interception, in order to establish (in a subsequent chapter) the importance of tillers to grain yield in canaryseed.

Chapter 5 The effect of seeding date on leaf appearance and tillering in annual canarygrass relative to spring wheat and oat in a semiarid environment.

5.1 Introduction

Annual canarygrass or canaryseed (*Phalaris canariensis* L.) is a small grain temperate cereal primarily produced in Canada, Thailand and Argentina (FAOSTAT, 2018). Its production in Canada and Argentina suffers from high grain yield instability among site-years of cultivation (Miller, 2000; Bodega et al., 2003; May et al., 2012a). Canaryseed grain has a finite market. It is almost solely used as an ingredient in feed mixtures for song birds. However, the absence of gluten-like proteins (Boye et al., 2013) and its recent approval for use in human food (Canaryseed Development Commision of Saskatchewan, 2018) is likely to increase the market potential of the crop.

A study by May et al. (2012a) addressed the importance of the environment on the grain yield variability among site-years of cultivation. Environmental factors can influence the development of a crop, especially in the genotypes that are not well adapted to the prevailing environmental conditions. Crop development in cereals is closely related to the number of leaves a plant forms on the main stems and the duration each leaf requires to fully expand. Leaf appearance rate (or phyllochron, the inverse of leaf appearance rate, often expressed in thermal time (Tt)), has been the subject of extensive research in cereals and other annual crops. There are studies which dealt with the hypothesis that temperature *per se*, at or near the seedling crown, is closely related to the phyllochron in wheat (Jamieson et al., 1995a; McMaster et al., 2003; Jamieson et al., 2008). Other studies suggested that differences in the phyllochron among different seeding dates (SDs) are associated with the day length, at seeding or emergence, in wheat (Baker et al., 1980; Wilhelm and McMaster, 1995) and oat (Sonego, 2000). Although these studies refer to different abiotic factors, their results suggest that environment affects the cereal phyllochron. In addition, other abiotic factors such as water or nutrient availability also influence phyllochron, and thus crop developmental responses to the environment, in barley (Arisnabaretta and Miralles, 2004), wheat (Salvagiotti and Miralles, 2007) and triticale (Estrada-Campuzano et al., 2008). To date, no information related to phyllochron has been reported for canaryseed. In light of the above findings the first objective of the present study was the investigation of canaryseed phyllochron and its change under different growing conditions.

An important morphological characteristic of cereals that is often studied in relation to main stem leaf appearance is the tillering pattern. In wheat and barley, main stem phyllochron has

been associated with tiller appearance (Klepper et al., 1982; Kirby et al., 1985). Evidence from a recent study (May et al., 2012a) suggests that a higher number of inflorescence-bearing tillers of early-sown canaryseed crops versus late-sown crops contribute disproportionally more to grain yield relative to the main stem inflorescence. The potential relative importance of the number of inflorescence-bearing tillers to crop grain yield might play a role in the high grain yield variability of canaryseed. The number of mature tillers that form an inflorescence and contribute to grain yield in cereal crops depends on the tillering pattern. The tiller number is the result of the total number of tillers formed minus those that senesce and do not form seeds. Both of these numbers depend on plant physiological processes (eg, assimilate availability and hormonal signaling) and environmental factors (eg, light signaling and intensity, nutrient availability) (Evers et al., 2011 and references therein). In addition, Steinfort et al. (2017) demonstrated that wheat isogenic lines differing in their vernalization and photoperiod sensitivity showed large variation in tiller number appearance and mortality. Therefore, it was hypothesized that the putative vernalization requirement of canaryseed, and the potential importance of tillers to crop grain yield are of interest in explaining the yield instability of the crop. The second objective of this study was to investigate the tillering pattern of canaryseed relative to spring wheat and oat.

5.2 Materials and methods

5.2.1 Plant material

For plant material information about four out of the five cultivars used in this study see section 4.2.1. One additional canaryseed cultivar was used in this study, namely CDC Togo, which was developed at the Crop Development Centre at the University of Saskatchewan in Saskatoon, Canada as a result of planned crosses using the first glabrous canaryseed cultivar, CDC Maria. In tables and/or figures, cultivar names may appear without the acronyms CDC and AC due to space limitations.

5.2.2 Growing conditions

For years and location of the field experiments, soil type and chemical analysis, fertilizer application and weed control see section 3.2.2.

5.2.3 Experimental set-up

For experimental design and seeding practices see section 3.2.3. For plot organization see section 4.3.2.1.

5.2.4 Observations and estimates

Crop emergence was recorded when at least 50% of the seedlings had emerged. It was limited to the 2013 and 2014 experiments and a single date was used for each species. Usually canaryseed cultivars emerged a day after the wheat and oat cultivars, except for the 2014 very late SD when the canaryseed cultivars emerged two days after the wheat and oat.

Observations and estimates were obtained from destructively harvested previously randomly selected and tagged plants for all five cultivars used in this study. In addition, more frequent, *in situ* observations were conducted and estimates obtained for the canaryseed cultivar CDC Bastia for comparison of the results derived from the two methods, the *in situ* and the destructive harvests. A few plants, but never more than two per plot, senesced prematurely and did not reach physiological maturity. Observations made after the plants were destructively harvested were omitted from the data.

Seedling leaf stage was determined using the modified Haun leaf scale based on the youngest leaf ($MHLS_{YL}$), as described in Chapter 3.

Time of appearance and death of tillers, as well as their subtending main stem leaf (point of tiller emergence), were recorded three times a week on the six pre-selected and tagged plants of CDC Bastia. For tiller identification, the coding system described by Klepper et al. (1982) was followed. Canaryseed plants of the cultivar CDC Bastia rarely produced coleoptilar tillers. Very few secondary tillers emerged on the plants of CDC Bastia and these data are not presented.

The tillering pattern of all five cultivars is presented for the early and late SDs only, for both years. The prevailing environmental conditions at the beginning of July, when very late-sown treatments emerged, caused substantial soil crusting, which resulted in lower plant population densities. That potentially caused different tiller appearance rates as has been shown in spring wheat by Evers et al. (2006 and references therein). Different tiller appearance rates, in turn, might have altered differentially the PAR level and the red to far-red ratio within the crop leaf canopy. Below-threshold values for both these factors (PAR level and red to far red ratio) allow tiller appearance while values at or higher than the threshold have been shown to cause tillering cessation in spring wheat. Data for the tillering pattern for all five cultivars and all SDs are reported as appendices. Given that in spring wheat, plant population density under full sunlight does not affect the plant developmental stage at the first tiller appearance (Evers et al., 2006), the lower population densities of the very late SDs is not expected to have caused differences in the onset of tillering. Estimates of the onset of tillering, in terms of Tt after crop appearance, were determined using two replications $block^{-1}$.

For the *in situ* observations, time of tiller appearance was recorded as the time between two consecutive measurements on the first of which the tiller was not visible and the second on which the tiller had already emerged above the preceding leaf sheath. Time of tiller death was determined based on the rank or the length of the youngest identified leaf and recorded as the time between two consecutive measurements on the last of which the rank and the length had not increased, relative to the previous measurement, and its preceding measurement (Evers et al., 2006).

Tiller number as well as point of appearance were also recorded for the destructively harvested seedlings from all five crop cultivars. Bilinear piecewise regression analyses (Ryan and Porth, 2007) were conducted between the tiller number and the Tt elapsed after crop emergence in order to estimate the onset of tiller appearance in terms of Tt, using the data from the destructively harvested seedlings for all five cultivars. In a few plots, mainly for wheat and oat determining the onset of tiller appearance was not feasible using the method described due to the nature of the data (only one or two tillers per plant emerged and thus, regardless of the frequency of the data collection, linear regressions were not feasible). In these cases, the procedure followed for the observations in the cultivar CDC Bastia was adopted instead. Cessation of tillering was estimated as the mid-Tt between the highest tiller number observation and its preceding one. Given that destructive sampling was conducted on randomly assigned sub-plots, highest tiller number observation was determined as the first in three (occasionaly two) consecutive observations of which the second and third were equal or lower than the first one. Occasionally, in oat and canaryseed, but rarely in wheat, tillering resumed before the plant reached a maximum tiller number. The term "maximum tiller number" will be used to describe this occurrence. Maximum tiller number was determined as the highest tiller number observation $plot^{-1}$ and tiller number at final harvest after harvesting six randomly pre-tagged plants $plot^{-1}$.

A comparison of the *in situ* and the destructive harvest methods for estimating the Tt of the cessation of tiller appearance in CDC Bastia is reported in the results section 5.3.3.

Main stem height was determined using a ruller. Bilinear piecewise regression analyses (Ryan and Porth, 2007) were conducted between the stem height and the Tt to estimate the start of stem elongation. Data from both the *in situ* observations on CDC Bastia and the destructively harvested seedlings for all five cultivars were used for that purpose. A comparison between the two methods in the estimation of the Tt of the start of stem elongation in CDC Bastia is reported in the results section 5.3.3.

Weekly light interception observations were conducted approximately at the second leaf stage (or at approximately 50% light interception for the early seeding date in 2013) in the central sub-plot of three replications block^{-1} (once for two replications block^{-1} and once for one replication block^{-1}, when weather conditions obstructed the process of *in situ* observation). Four, 10-cm apart, individual measurements were made at the bottom of the sub-plot canopy, perpendicularly oriented to the seedling rows. Each measurement was conducted simultaneously with an observation at the top of the canopy at the end of the sub-plot using two 1-m line quantum sensors (LI-191SA, Li-COR, Lincoln, NE) attached to a data-logger (LI-1400, Li-COR, Lincoln, NE) on clear sunny days between 12:00pm and 2:00pm. Periodical destructive LAI observations were subjected to non-linear regression analyses using the Beta growth function (Yin et al., 2003)

$$\%IPAR = \%IPARmax\left(1 + \frac{Tte-Tt}{Tte-Ttm}\right)\left(\frac{Tt}{Tte}\right)^{\frac{Tte}{Tte-Ttm}} \quad \text{(Equation 5.1)}$$

where %IPAR is the percentage of PAR intercepted and Tt is the thermal time elapsed from crop emergence. The model returns estimated Tt at which the maximum rate of change of %IPAR is attained (Ttm), the Tt at which the maximum %IPAR is reached (Tte) and the maximum percentage of IPAR (%IPAR$_{max}$). The method was followed to investigate potential differences in the percentage of PAR interception by the crop at the cessation of tiller appearance. Crop stage was estimated from the Tt and the phyllochron as described below.

Observations from the modified Haun leaf stage based on the youngest leaf lamina length (MHLS$_{YL}$) were used for the phyllochron estimates as explained in Chapter 3 – section 3.2.4. Phyllochron was estimated as the reciprocal of the slope of the relationship between MHLS$_{YL}$ and Tt for all five cultivars. After plotting the data obtained from the cultivar CDC Bastia for each experimental plot year × SD × block separately, a bilinear (or even a trilinear, in the early SD in 2014) relationship was identified. Phyllochron was estimated for each of the linear segments according to Ryan and Porth (2007)

$$MHLS_{YL} = a_1 + b_1 Tt(Tt \leq BP) + b_1 BP(Tt > BP) + b_2(Tt - BP)(Tt > BP) \quad \text{(Equation5.2)}$$

where a_1 is the $MHLS_{YL}$ at crop emergence, b_1 is the slope of the first linear segment and its inverse is the phyllochron of the leaves emerged prior to the intersection of the linear segments, BP is the Tt at the intersection of the linear segments called Break Point, and b_2 is the slope of the second linear segment while its inverse is the phyllochron of the leaves emerged past the intersection of the linear segments. “Phyl.i” and “phyl.ii” are used to describe the average phyllochrons of the leaves prior to and past the intersection of the linear segments, respectively.

In the case of the early seeding in 2014 when three linear segments were identified, phyl.ii was estimated as the mean phyllochron of the leaves past the first BP.

The phyllochron of the other four cultivars was again obtained as the reciprocal of the slope of the relationship between $MHLS_{YL}$ and Tt, from simple linear regressions. Three (some entries in late SD in 2014) to five data points were used in the regressions. Given the relatively low number of data points in the estimation of the phyllochron of the other four cultivars, and the relatively late first determination of leaf stage (close or past the second leaf stage), potential bilinear relationships between $MHLS_{YL}$ versus Tt would not be feasible. In this case an average phyllochron was estimated. Scatter plots did indicate bilinear relationsips in very few cases. FLN was obtained as described in section 4.2.4.1.

Rainfall and temperature records were obtained as described in section 3.2.4.2. Estimates of daily incoming solar radiation were obtained from the Thornton-Running solar radiation prediction model (Ball et al., 2004) using the data from the weather stations. Information regarding the air temperature, rainfall, thermal time and incoming solar radiation throughout the crop cycles is presented in figure 3.1. The daily accumulated thermal time in degree-days was calculated as described in section 3.2.4.2.

5.2.5 Data analysis

Estimates from piecewise regressions related to phyllochron change ($MHLS_{YL}$ and Tt), phyli., phyl.ii, average phyllochron, the onset of tiller appearance, the start of stem elongation, the FLN, Beta function estimates, average tiller appearance duration, average elapsed Tt between the appearance of consecutive tillers, maximum tiller number and that at final harvest and tiller mortality were analyzed in the PROC GLIMMIX of SAS v9.4 (SAS Institute, 2013) by year × SD or year × cultivar combinations. In each combination, block × replication random effect was controlled for heterogeneity of residual variances using the subject option in the random statement of PROC GLIMMIX (Stroup, 2014). For comparison and separation of means and normality of errors see section 4.2.5. When data from only the first two SDs were compared, means within cultivars and years were subjected to appropriate t-tests and significance was determined at the 5% level while removal of potential outliers was conducted based on the model for the analysis of cultivar effect within year × SD combinations. Only mean values are provided for data presented in percentages or frequencies.

5.3 Results

5.3.1 Leaf appearance

The overlapping appearance of main stem leaf laminae in canaryseed first reported in Chapter 3 was quantified for three canaryseed, one spring wheat and one oat cultivar, using a different method from that described in section 3.2.4. The lamina length of the reference leaf used for the $MHLS_{YL}$ determination was often shorter than its ultimate one in all three canaryseed cultivars (Figure 5.1). The lamina at the time of observation had often emerged by 70 to 80 percent but values as low as 60 were also recorded. No systematic differences in the length of the reference leaf lamina were observed among the canaryseed cultivars at the time of observation. However, differences were detected between canaryseed, and wheat and oat. The length of the reference leaf lamina at the time of observation in wheat was equal or similar to its ultimate length. In oat, the reference leaf lamina was also near its ultimate length but usually exhibited an intermediate pattern between wheat and canaryseed.

The relationship between $MHLS_{YL}$ and the Tt for the canaryseed cultivar CDC Bastia seeded at three dates in 2013 and 2014 is presented in Figure 5.2. Plotted observations indicate that $MHLS_{YL}$ and Tt are not related in a linear fashion in any of the six SD × year combinations (the term "environment" will be used hereafter). A distinct change in the slope of the relationship between the two variables occurs between the first and second $MHLS_{YL}$. In addition, with the early seeding in 2014 a second change in the slope is indicated close to the sixth $MHLS_{YL}$. Analyses for each of the environment × block × replication combinations (48 in total) revealed that relationships between the two variables were significant ($P < 0.001$) and better described by bilinear (or trilinear) models, rather than linear or power equations (based on the standard error of the models).

FLN on CDC Bastia main stems was significantly ($P < 0.001$) increased with delayed compared to early seeding, except for the late seeding in 2014 (Table 5.1).

There were significant ($P < 0.05$ and $P < 0.001$ in 2013 and 2014, respectively) differences among SDs within years in the break point of the relationship between $MHLS_{YL}$ and the Tt which was estimated to occur (Tt_{BP}) (Table 5.1). However, the pattern of the differences among the SDs was not consistent between the two years. Nevertheless, the Tt_{BP} ranges corresponded to similar $MHLS_{YL\_BP}$ values among SDs.

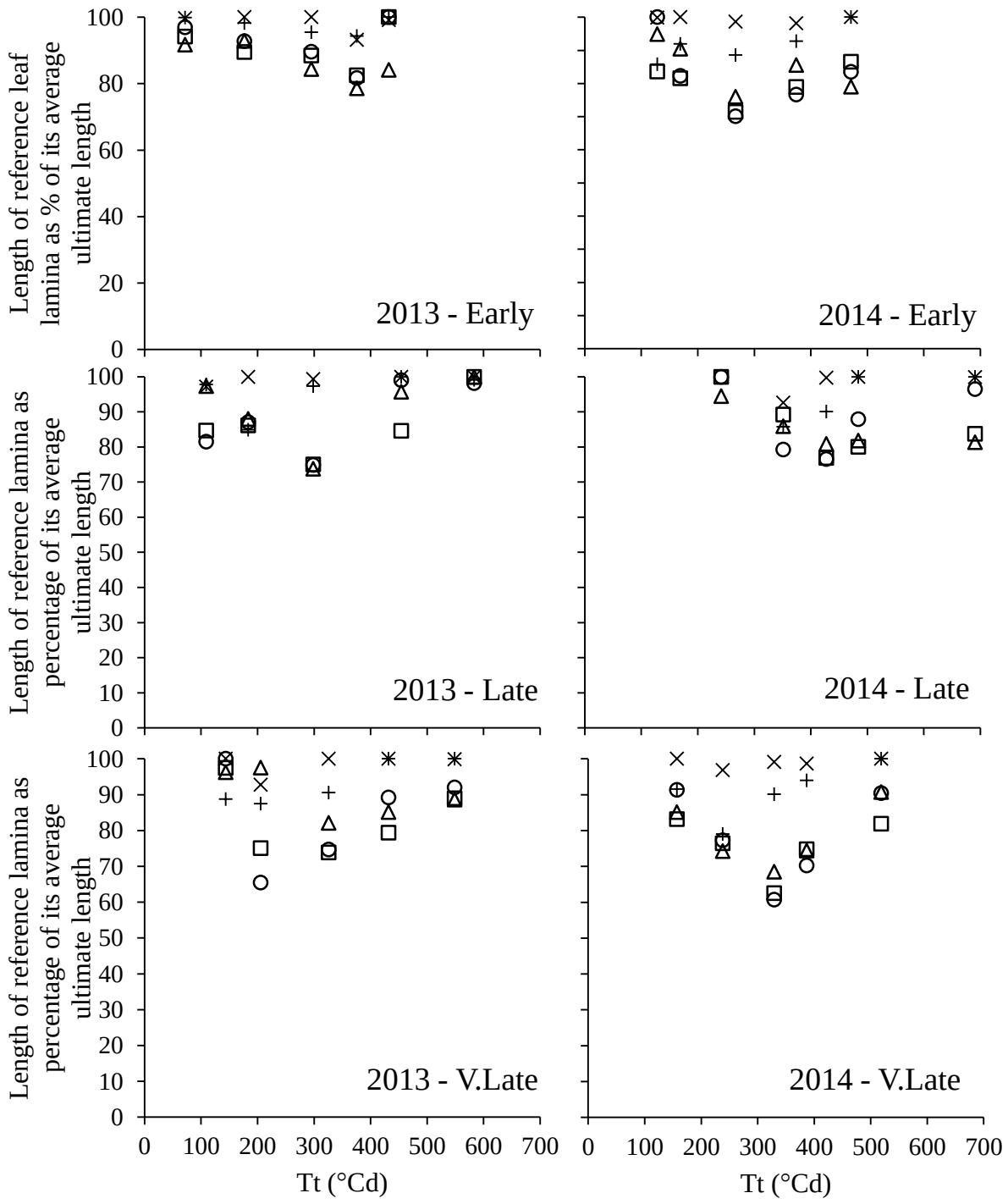

Figure 5.1. Length of reference leaf lamina in Haun leaf stage determination as percentage of its average ultimate length versus the thermal time elapsed from crop emergence (Tt) for wheat ('×' sign), Oat ('+' sign) and the canaryseed cultivars CDC Bastia, CDC Togo and Keet (circle, square and triangle, respectively) when seeded early, late and very late in 2013 and 2014, respectively. Data points are derived from observations on two blocks seeding date^{-1}, four replications block^{-1} and six plants replication^{-1}.

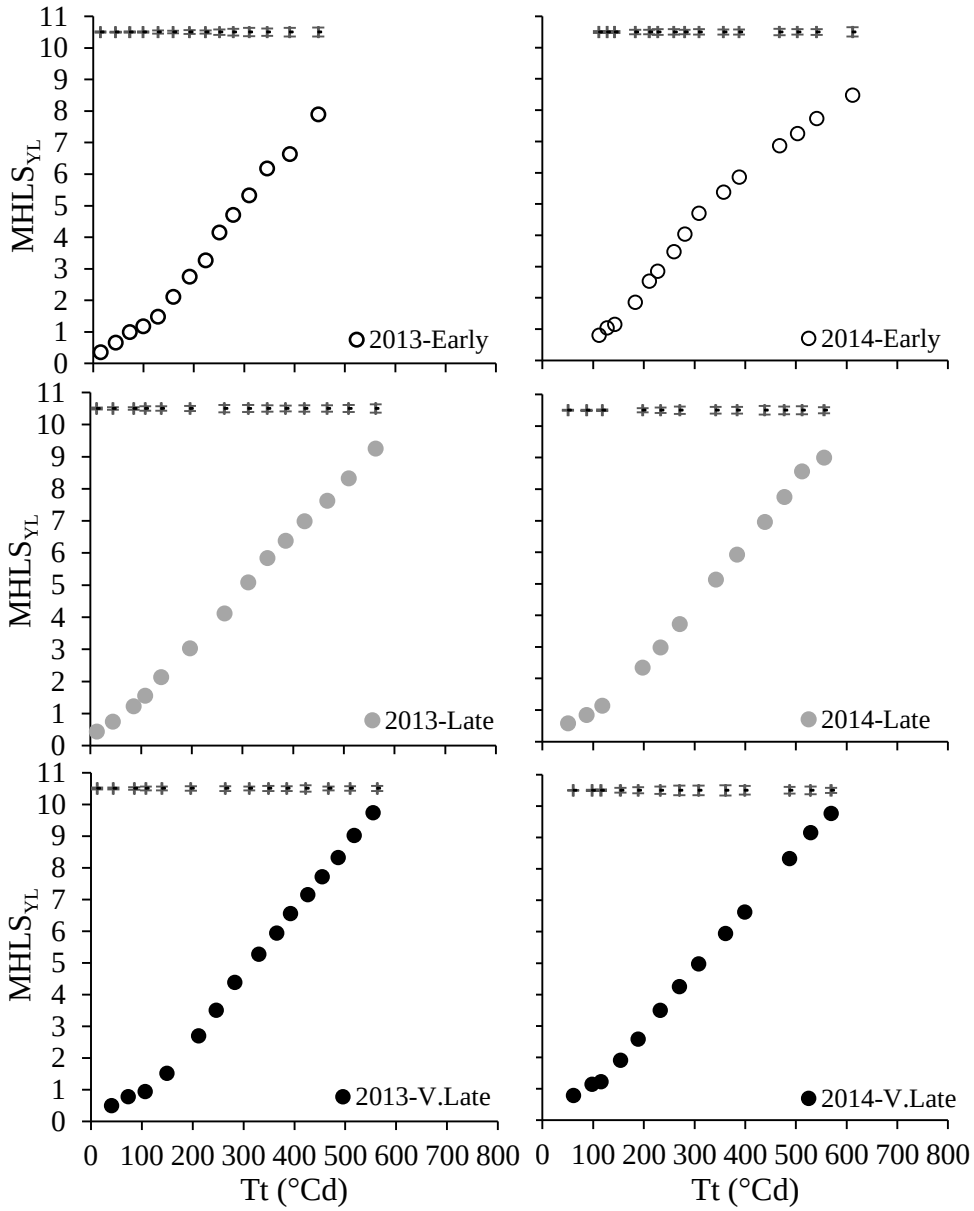

Figure 5.2. Mean modified Haun leaf stage ($MHLS_{YL}$) versus the thermal time elapsed from crop emergence (Tt) for the canaryseed cultivar CDC Bastia when seeded early (A and D), late (B and E) and very late (C and F) in 2013 and 2014, respectively. Each data point is derived from observations on two blocks seeding date^{-1}, four replications block^{-1} and six plants replication^{-1}. Vertical bars indicate standard error.

Significantly ($P < 0.01$) different phyllochrons (i and ii) were found with one or both later SDs when compared to the early SD. In addition, phyl.ii was substantially (32 to 66%) less compared to phyl.i. With later seeding, differences were larger, mainly due to the increased phyl.i relative to that with the early SD.

Table 5.1. Final leaf number (FLN), estimated modified Haun leaf stage at which phyllochron changed ($MHLS_{YL\_BP}$), thermal time from emergence when the break point (BP) occurred and phyllochron prior to (phyl.i) and past (phyl.ii) the BP for the canaryseed cultivar CDC Bastia when seeded on three dates in 2013 and 2014.

Response variable	2013					2014				
	Stat. An.[1]									
	Early	Late	V.Late	SEM[2]	St.Sign.[3]	Early	Late	V.Late	SEM	St.Sign.
FLN	8.4	**10.3**	**12.6***	0.14	***[5]	8.6	9.2	**11.1***	0.22	***
$MHLS_{YL\_BP}$	1.5	**1.1**	**1.1**[4]	0.08	*	1.4	1.3	1.3	0.04	ns
Tt_{BP}	124.8	**91.8**	129.4*	9.67	*	160.3	145.1	**123.9***	5.33	***
Phyl.i	102.5	100.9	**144.4***	9.28	**	92.3	**117.7**	**118.3**	5.78	**
Phyl.ii	49.4	**58.5**	49.2*	1.61	***	62.7	**51.0**	**50.8**	1.48	***

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance

[4] Seeding date means in bold differ significantly from the early seeding date mean within a year × response variable combination. Very late mean followed by an asterisk differ significantly from the late mean within a year × response variable combination. Mean separations were conducted by Tukey's tests.

[5]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × response variable combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.

Average phyllochron of canaryseed cultivars appeared to be substantially and significantly ($P < 0.001$) lower than that of wheat in almost all tested environments and compared to that of oat in half of the tested environments (Table 5.2). For the average phyllochron for each canaryseed cultivar across environments, late seeding generally resulted in significantly ($P < 0.01$) higher values compared to those with early and/or very late SDs.

Table 5.2. Estimated average phyllochron for canaryseed, spring wheat and oat cultivars seeded on three dates in 2013 and 2014.

Cultivar	Stat.An.[1]				Stat. An[4]. SEM	Sign.				Stat. An. SEM	Sign.
		2013					2014				
		Early	Late	V.Late			Early	Late	V.Late		
Togo		48.3b	**60.5b**	**53.4b*[5]**	0.86	***[6]	56.2b	**69.3a**	57.9b*	1.35	***
Bastia		52.4b	**61.1b**	53.6b*	1.24	***	60.7ab	**69.2a**	**52.7b***	2.09	***
Keet		53.0b	57.6b	57.3b	1.65	ns	56.5b	**66.4a**	59.7b*	1.84	**
Barrie		72.5a	77.6a	73.7a	2.47	ns	67.1a	75.6a	75.2a	2.98	ns
Morrison		70.2a	72.6a	**57.2b***	1.83	***	59.9b	66.8a	59.7b	3.18	+
	SEM[2]	1.27	1.95	2.19			1.71	2.76	2.58		
	Sign.[3]	***	***	***			***	ns	***		

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Statistical analysis for the seeding date means within a year × cultivar combination. [5] Seeding date means in bold differ significantly from the early seeding date mean within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [6]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.

5.3.2 Tillering pattern in the canaryseed cultivar CDC Bastia

5.3.2.1 Tiller number dynamics

Tillering of canaryseed plants started near the time that the fourth main stem leaf tip appeared in all four environments (Figure 5.3-A). In spite of the apparently similar tiller appearance rates (the slope of the near-linear part of the relationship illustrated in Figure 5.3) between within-year SDs, there were differences in the tillering pattern between environments across and within years.

Tiller appearance in plants seeded early in 2013 continued up to approximately the full expansion of the flag leaf lamina. At that point, the plants had initiated just over three viable tillers, which was the maximum tiller number. In contrast, plants seeded late in 2013 continued initiating tillers up to approximately the appearance of the seventh main stem leaf. That leaf stage was about three leaf stages prior to the expansion of the flag leaf. Consequently, late-sown plants in 2013 initiated just over 1.5 tiller in total, which was just half of the maximum tiller number initiated on the early-seeded plants in the same year. Given the similar tiller appearance rate mentioned earlier, the difference in the tiller number between the SDs in 2013 is primarily due to the shorter tiller appearance phase of the late-seeded plants. The difference in the length of the tiller appearance duration between the SDs in 2013 was in terms of both $MHLS_{YL}$ and Tt, as shown in Figures 5.3-A and B, respectively.

The tiller appearance pattern in 2014 was different from that observed in 2013. The tillering pattern of plants seeded on different dates in 2014 was similar up to approximately the attainment of the maximum viable tiller number. This occurred just after the initiation of the penultimate leaf tip for both SDs. Given the small numerical difference in the FLN of the treatments, the maximum tiller number was reached about a leaf stage later for late-sown plants compared to the early-seeded plants. After a maximum tiller number was reached for the two SDs, viable tiller number either started decreasing immediately or after it had remained nearly constant for some time (Figure 5.3-B).

In 2013, viable tiller number for both SDs decreased after reaching a maximum value by approximately one unit before a constant tiller number was reached. This was equal to 2.2 and 0.8 tillers $plant^{-1}$ in early and late seeding, respectively. Similarly, the early-seeded plants in 2014 reduced their viable tiller number, after they had reached a maximum value, by approximately one unit. In contrast, late-seeded plants in 2014 resumed main stem tiller appearance after they had temporarily reached a maximum value. Appearance of new viable main stem tillers occurred primarily from higher leaf axils such as T5 to T7 (Table 5.3). The

number of new viable initiated tillers was more than one plant^{-1}, however, the simultaneous senescence of a number of lower main stem ranked tillers resulted in an absolute increase of viable tiller number of one unit. Therefore, the final tiller number plant^{-1} of early and late-seeded plants in 2014 was 1.8 and 3.1, respectively.

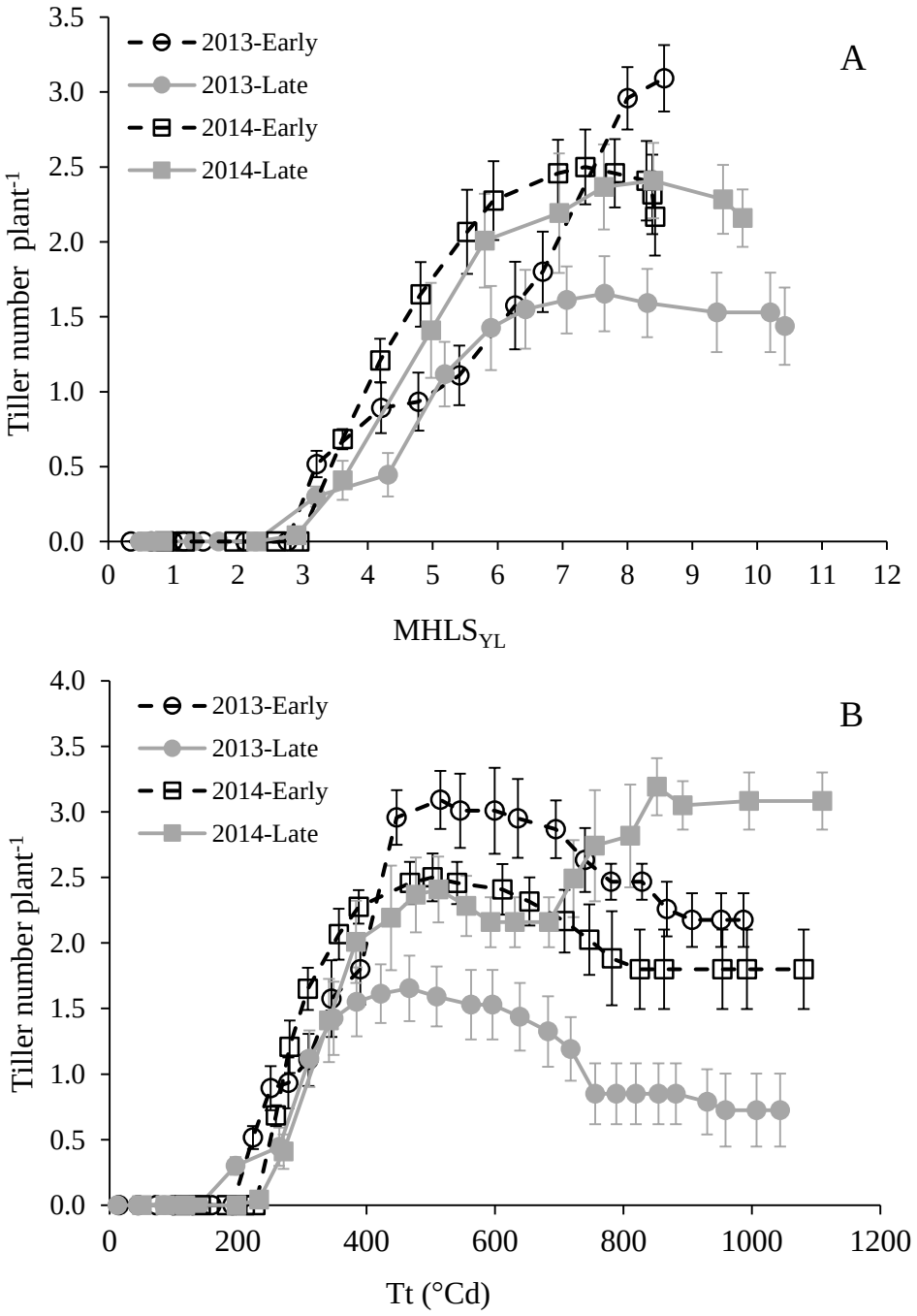

Figure 5.3. Tiller number plant^{-1} versus the modified Haun leaf stage ($MHLS_{YL}$) prior to the flag leaf ligule appearance (A) and versus the elapsed thermal time from crop emergence (Tt) (B) for the canaryseed cultivar CDC Bastia when seeded early (empty symbols) and late (closed symbols) in 2013 (circles) and 2014 (squares). Mean values are derived from observations conducted on two blocks seeding date^{-1}, two replications block^{-1} and six plants replication^{-1}. Symbols associated with data points where visible indicate standard error.

Differences between environments within years in the leaf stage at which main stem tillers appeared were detected but were inconsistent (Figure 5.4). The highest detected differences were between the early-seeded plants of the two years for T2 and T3. For both tillers, early-seeded plants in 2013 showed delayed appearance of these tillers by 1.0 and 1.5 leaves compared to early-seeded plants in 2014.

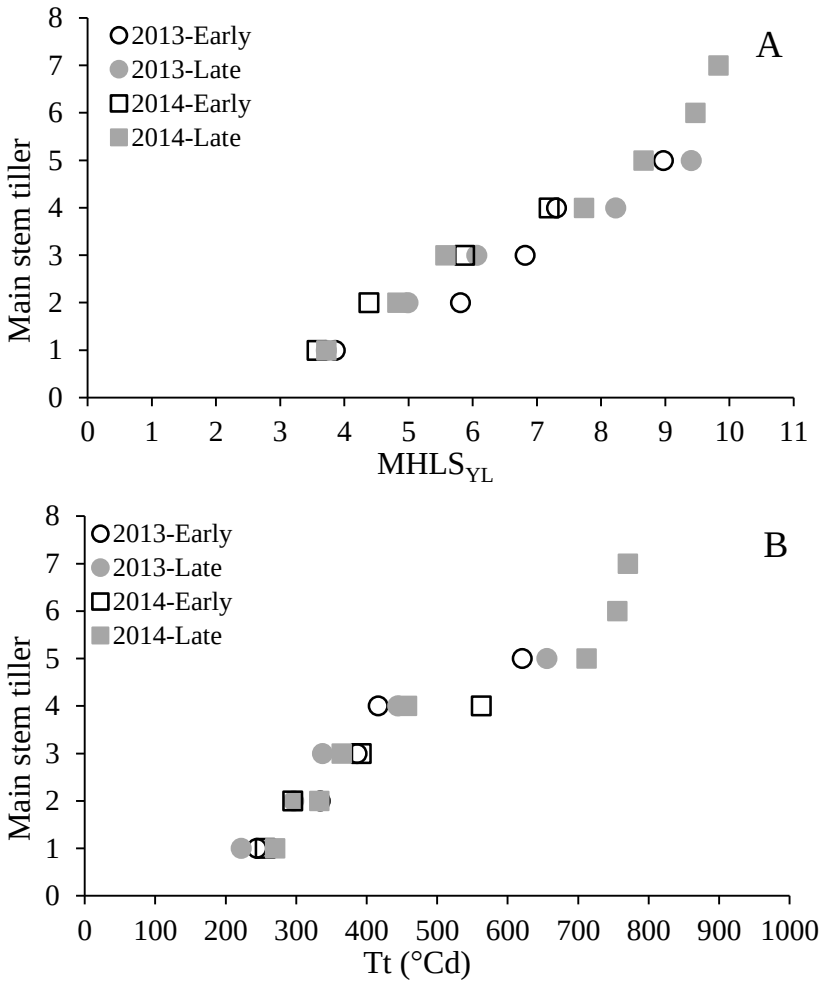

Figure 5.4. Modified Haun leaf stage ($MHLS_{YL}$) (A) and elapsed thermal time from crop emergence (Tt) prior to flag leaf ligule appearance (B) at the appearance of the main stem tiller (T1 to T7) for the canaryseed cultivar CDC Bastia when seeded early (empty symbols) and late (closed symbols) in 2013 (circles) and 2014 (squares). Mean values are derived from observations conducted on two blocks seeding date^{-1}, two replications block^{-1} and six plants replication^{-1}.

Differences illustrated in Figure 5.4 for T4 and higher ranked primary tillers should be considered with caution as the percentages of plants on which these tillers appeared were highly inconsistent (Table 5.3).

5.3.2.2 Point of tiller appearance

Almost all observed early-seeded plants but only half of the late-seeded ones initiated T1 (Table 5.3). Appearance of T2 occurred for almost all plants, regardless of the SD. Appearance of T3 was more variable among SDs. T3 appeared on nearly half of the early-seeded plants in both years but its appearance with late-seeded plants was more variable among late SDs. T4 appeared on a very low proportion of the tagged plants, except for the early SD in 2013. T5 and higher order main stem tillers did not appear or appeared on a very low percentage of the monitored plants, except for the late SD in 2014 where they appeared on a higher proportion of the observed plants, based on their order on the main stem.

Table 5.3. Percentage of plants of the canaryseed cultivar CDC Bastia on which the main stem tillers T1 to T7 visibly appeared above the enclosing leaf sheath when seeded on two dates in 2013 and 2014.

Main stem tiller	Seeding date			
	2013		2014	
	Early	Late	Early	Late
T1	96	58	88	54
T2	78	79	83	83
T3	57	26	58	75
T4	61	5	8	17
T5	17	11	0	21
T6	0	0	0	42
T7	0	0	0	46

[1] Percentages are derived from pooled observations on two blocks seeding date^{-1}, two replications block^{-1} and six tagged plants replication^{-1}.

5.3.2.3 Percentage of intercepted PAR (%IPAR)

The course of %IPAR over the Tt for the early and late SDs in 2013 were similar (Figure 5.5-A). In addition, the estimated parameters of the fitted curves were not significantly different (Table 5.4). Consequently, the fitted Beta sigmoid curves almost overlap each other. In contrast to 2013, the course of the %IPAR over the Tt for the early and late SDs in 2014 was slightly different (Figure 5.5-B). The data points for the late SD were often lower than that of the early SD. In addition, the unrestricted estimated parameters of maximum increase in the rate of the %IPAR and Tt to the maximum %IPAR of the fitted curves were slightly but significantly ($P < 0.05$) different. Based on these parameters, late SD had a delayed maximum increase in the rate of the %IPAR but a slightly shorter Tt to the maximum %IPAR relative to the early SD. Consequently, the fitted Beta curve of the late SD was shifted slightly downward compared to the early SD.

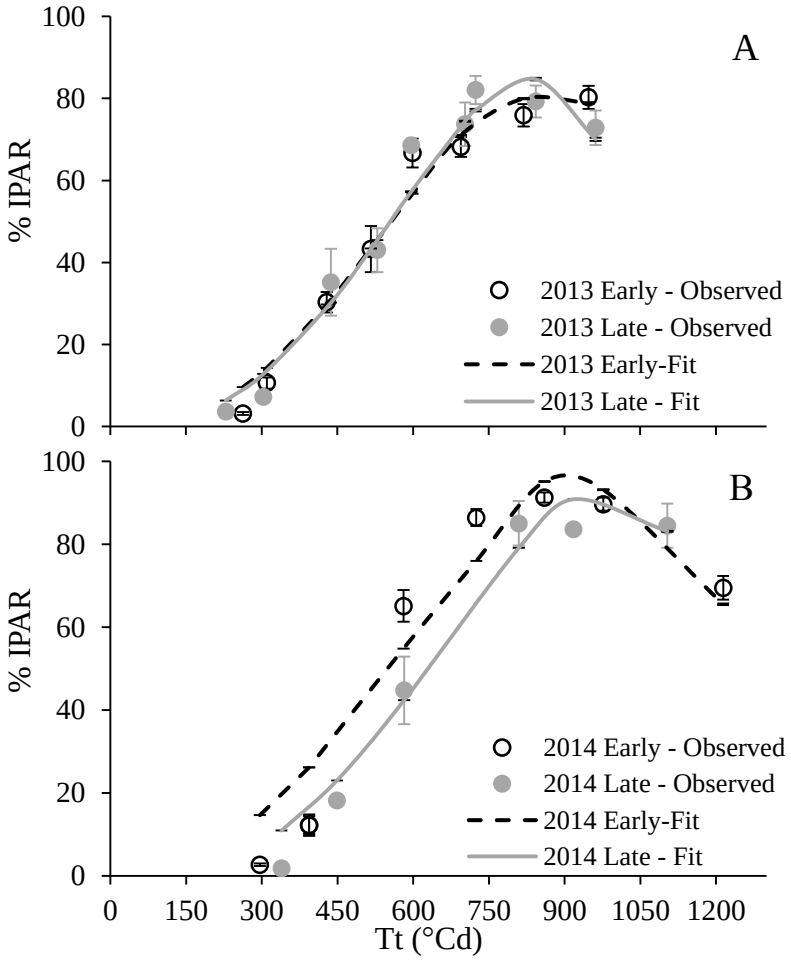

Figure 5.5. Mean observed values and Beta sigmoid function fit of the percentage of intercepted photosynthetically active radiation (%IPAR) versus the thermal time elapsed from crop emergence (Tt) for the canaryseed cultivar CDC Bastia when seeded early (empty symbols – black dashed line) and late (closed symbols – grey solid line) in 2013 (A) and 2014 (B). For further symbol explanations, see the figure legends. Symbols associated with the data points represent standard error. For more details concerning the model fit, see Appendix 3.

Table 5.4. Beta function estimates of the thermal time from crop emergence when the rate of change of the percentage of intercepted photosynthetically active radiation (PAR) reached the maximum value (Tt_m), the thermal time when the percentage of intercepted PAR reached the maximum value (Tt_e) and the maximum percentage of intercepted PAR ($\%IPAR_{max}$) for the canaryseed cultivar CDC Bastia when seeded on two dates in 2013 and 2014.

Estimated parameter	2013			2014		
	Early	Late	Sign.[2]	Early	Late	Sign.
Tt_m	547(10.8)[1]	554(31.7)	ns	584(19.2)	656(21.4)	*
Tt_e	864(128)	829(13.6)	+	1008(4.7)	983(6.4)	*
$\%IPAR_{max}$	85(1.5)	86(3.2)	ns	100(0)[3]	93(2.0)	-

[1] Values in parentheses represent standard error; [2] Statistical significance; [3] The estimate of 100 and the zero value for standard error are the results of the restricted parameter values to a maximum of 100 in the model-fitting process as that was exceeding the value of 100.

ns, +, *, ** and *** used to denote that the statistical significance is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. Means separation conducted with Tukey test.

5.3.2.4. Start of stem elongation

Differences in the start of stem elongation in CDC Bastia ranged between 26 and 170°Cd among SDs within years (Table 5.5). In general, stem elongation started significantly ($P < 0.01$) later, in terms of Tt, with late and/or very late SDs, compared to early SDs.

Table 5.5. Elapsed thermal time from crop emergence (Tt) (°Cd) at the start of stem elongation (SSE) for the canaryseed cultivar CDC Bastia when seeded on two dates in 2013 and 2014.

Response variable	2013					2014				
				Stat. An.[1]					Stat. An.	
	Early	Late	V.Late	SEM[2]	St.Sign.[3]	Early	Late	V.Late	SEM	St.Sign.
Tt at SStEl	356[1]	**465**	**526*[4]**	8.2	***[5]	446	472	**538**	19.2	**

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [4] Seeding date means in bold differ significantly from the early seeding date mean within a year. Very late mean followed by an asterisk differ significantly from the late mean within a year. Mean separations were conducted by Tukey's tests. [5]** and *** used to denote that the statistical significance within a year year is ≤0.01 and ≤0.001, respectively.

Comparison of the two different methods of determination of the start of stem elongation, the *in situ* and the destructive harvests provided a significant ($P = 0.0126$) simple linear regression model, which explains 82% of the data variation (Figure 5.6). In addition, the near unity slope of the model, which almost coincides with the 1:1 line, demonstrates that the method involving the destructive harvests was sufficient to generate similar results compared to those from the more frequent *in situ* observations. Therefore, the method of destructive observations was employed for the determination of the start of stem elongation in all five crop cultivars.

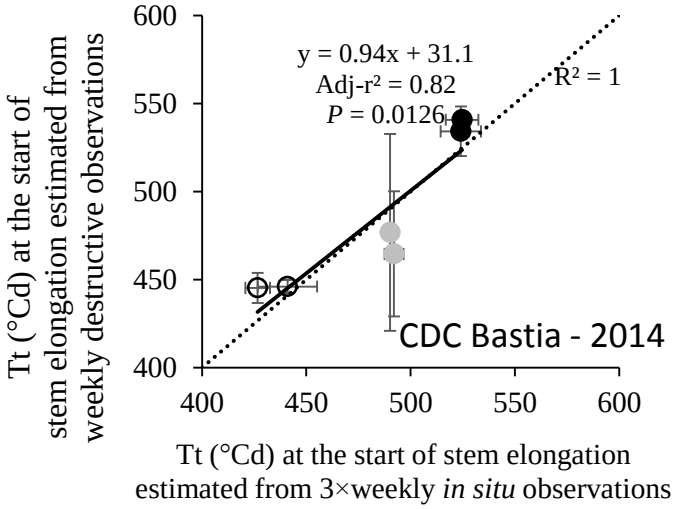

Figure 5.6. Comparison of the estimates of the thermal time from crop emergence (Tt) at the start of stem elongation obtained from two methods, the 3×weekly *in situ* observations and the weekly destructive observations, for the canaryseed cultivar CDC Bastia when seeded early (open symbols), late (closed grey symbols) and very late (closed dark symbols) in 2014. Each data point represents the mean from an experimental block, four replications block^{-1} and six randomly selected plants replication^{-1}. Dashed line represents 1:1. Symbols associated with data points represent standard error.

5.3.2.5 Cessation of tiller appearance

Cessation of tiller appearance in all four environments was estimated to have occurred between the initiation of the sixth and the eighth leaf (Figure 5.7-A). The differences between SDs within years were relatively small. In 2013, the differences were significant ($P < 0.05$) while late-seeded plants terminated tiller appearance 1.5 leaves earlier compared to the early-seeded plants. In 2014, the difference in the $MHLS_{YL}$ at which tiller number reached a maximum value between the SDs was one leaf. This was the reverse of the trend observed in 2013 and statistically non-significant. Prior to flag leaf appearance, the estimated elapsed Tt to the cessation of tillering was similar to that described for the $MHLS_{YL}$ (Figure 5.7-B). Late-seeded plants in 2013 ceased tiller appearance 80°Cd (a few days) earlier compared to early-seeded plants in the same year. With the two SDs in 2014, plants ceased their tiller appearance at almost the same Tt. However, late-seeded plants resumed their tiller appearance past the flag leaf appearance. Those plants grew on average one more non-senescing tiller before reaching a maximum tiller number and consequently significantly ($P < 0.001$) delayed the cessation of tiller appearance by almost 400°Cd (Figure 5.3-B). This was approximately 850°Cd from crop emergence and coincided with mid-anthesis.

Cessation of tillering in three out of four environments was estimated to have occurred when %IPAR by the leaf canopy of the plot was near 35, based on both phenological phases prior to and past flag leaf appearance (Figure 5.8). With late seeding in 2014, cessation of tillering occurred at a somewhat lower %IPAR compared to the other three environments. These plants grew higher order main stem tillers, after flag leaf appearance and the maximum tiller number was attained when %IPAR had reached a value greater than 80.

Comparison of the two different methods used to estimate the Tt at the cessation of tiller appearance, the *in situ* and the destructive harvests provided a significant ($P = 0.003$) simple linear regression model, which explains 56% of the data variation (Figure 5.9). In addition, the near unity slope of the model demonstrates that the method involving the destructive harvests was sufficient to generate similar results compared to those from the more frequent *in situ* observations. Therefore, the method of destructive observations was employed for the determination of the cessation of tiller appearance in all five crop cultivars.

Tt at the cessation of tillering was correlated with the Tt at the start of stem elongation (Figure 5.10). The two variables were linearly associated. Interestingly, the data points corresponding to the two blocks from the late SD in 2014, which showed tillering cessation at low %IPAR, do not seem to fall out off the relationship. In contrast, the data point from one block from the early SD in 2013 deviated from the relationship and was excluded.

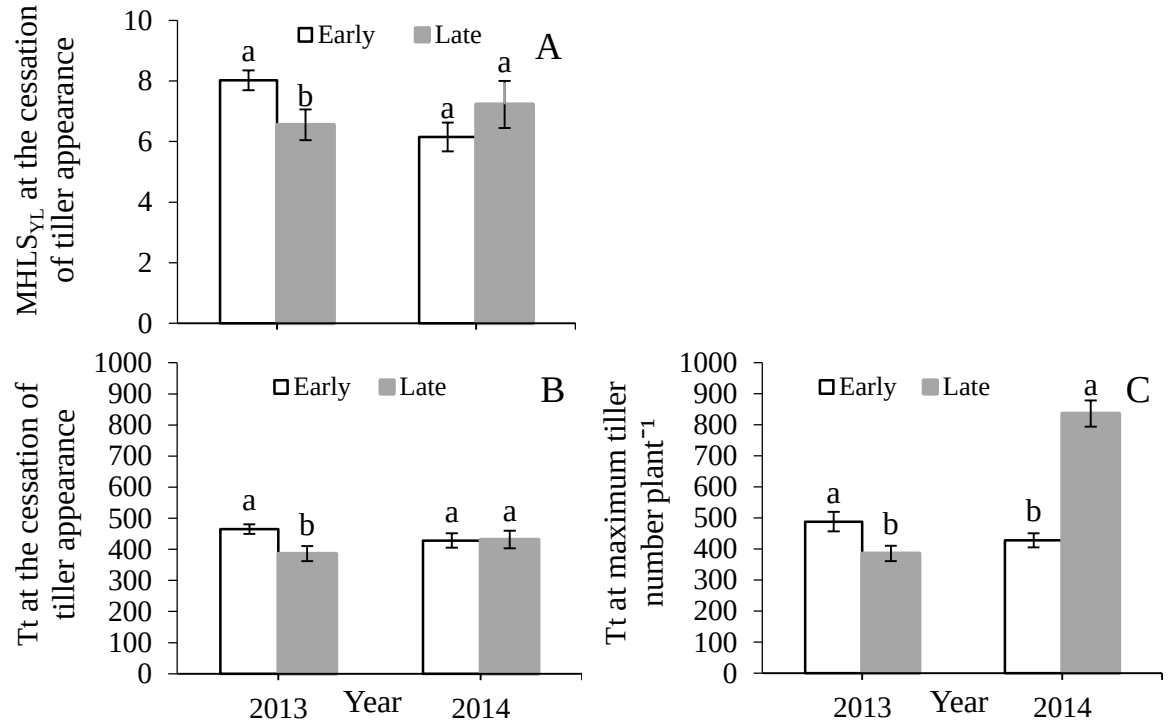

Figure 5.7. Modified Haun Leaf Stage (MHLS$_{YL}$) (A) thermal time from crop emergence (Tt) prior to (B) and after flag leaf appearance (C) at the cessation of tiller appearance / maximum tiller number plant^{-1} for the canaryseed cultivar CDC Bastia when seeded early (empty bars) and late (closed bars) in 2013 and 2014. Means are derived from two blocks seeding date^{-1}, two replications block^{-1} and six plants replication^{-1}. Means within a year and a response variable followed by the same letter do not differ significantly ($P > 0.05$). Mean separations were conducted by appropriate *t*-tests (see Appendix 4 for more details). Symbols at the top of the bars indicate standard error.

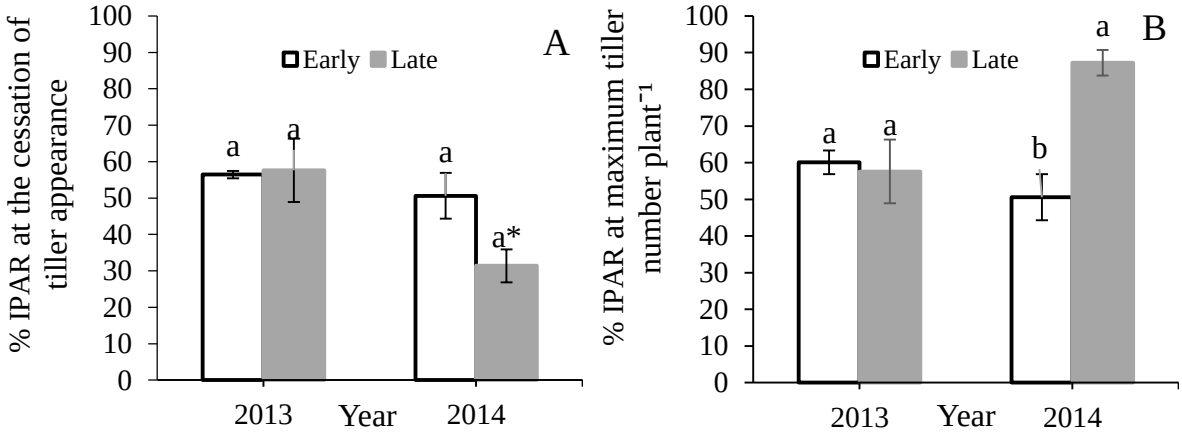

Figure 5.8. Percentage of intercepted photosynthetically active radiation (%IPAR) at the cessation of tiller appearance (A) and maximum tiller number plant^{-1} (B) for the canaryseed cultivar CDC Bastia when seeded early (empty bars) and late (closed bars) in 2013 and 2014. Mean values are derived from two blocks seeding date^{-1} and one or two replications block^{-1} (three or four replications in total). Means within a year and a response variable followed by the same letter do not differ significantly ($P > 0.05$). Mean separations were conducted by appropriate *t*-tests (see Appendix 5). Symbols at the top of the bars represent standard error. *$P < 0.1$.

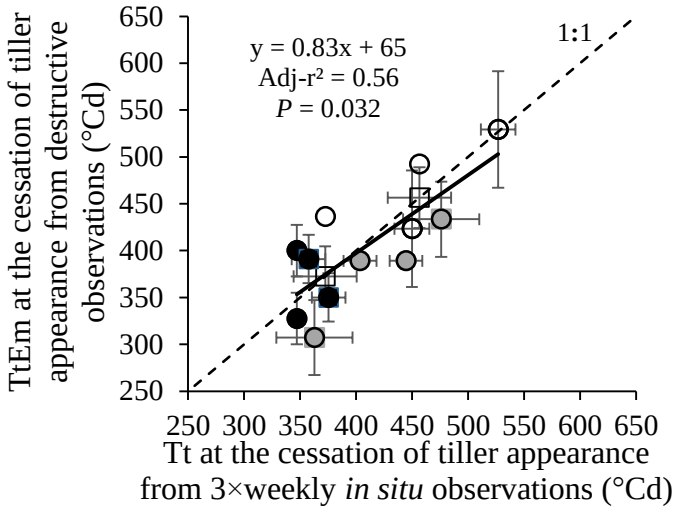

Figure 5.10. Comparison of the estimates of the thermal time from crop emergence (Tt) at the cessation of tiller appearance obtained from two methods, the 3×weekly *in situ* observations and the weekly destructive observations, for the canaryseed cultivar CDC Bastia when seeded early and late in 2013 and 2014. Each data point represents the mean of an experimental block, two to four replications block^{-1} and six randomly selected plants replication^{-1}. Dashed line represents 1:1. Symbols associated with data points represent standard error.

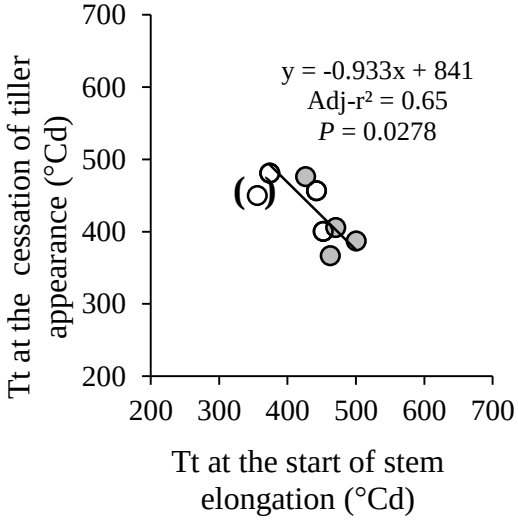

Figure 5.9. Thermal time from crop emergence (Tt) at the cessation of tiller appearance versus that at the start of stem elongation for the canaryseed cultivar CDC Bastia when seeded early (open circles) and late (dark circles) in 2014. Each data point represents the mean from an experimental block and is derived from two replications, each of which is the mean value of six randomly selected plants. The data were obtained from the 3×weekly *in situ* observations.

5.3.3 Comparison of the tillering pattern among five crop cultivars– Observations on destructively harvested seedlings

5.3.3.1 Tiller number patterns

Based on MHLS$_{YL}$

Tillering in all three canaryseed cultivars started near the time of the appearance of the fourth main stem leaf (Figure 5.11). In contrast, tillering in wheat and oat started earlier, near to or

between the appearance of the second and third main stem leaf. Tiller appearance in canaryseed continued at least up to the time of flag leaf emergence in most of the environment × cultivar combinations (Figure 5.11). In contrast, the oat cultivar initiated all tillers prior to the time of flag leaf emergence or even around the fourth or fifth leaf stage in most environments. The wheat cultivar had a tillering pattern similar to that of the oat and similar to that of the canaryseed cultivars in 2013 and 2014, respectively.

An accurate estimate of an average tillering rate (number of tillers emerged main stem leaf^{-1}) prior to the cessation of tiller appearance was restricted by the relatively low number of observations prior to the full expansion of the flag leaf and the non-linear pattern of tiller appearance versus the $MHLS_{YL}$. However, average tillering rate main stem leaf $^{-1}$ was higher in wheat compared to most canaryseed and oat environment × cultivar combinations based on the hypothetical slope of the relationship between tiller number and $MHLS_{YL}$ (Figure 5.11). The average tillering rate main stem leaf $^{-1}$ of all three canaryseed cultivars was higher with the late compared to the early seeding date in 2013. In contrast, in 2014, differences in the average tillering rate between early and late seeding of canaryseed and wheat were small.

Based on Tt

Differences in the onset of tillering for canaryseed between SDs within years and cultivars were not significant (Table 5.6). In wheat and oat, significant ($P < 0.05$) or near significant ($P < 0.1$) differences were observed between SDs in both years (Table 5.6).

Table 5.6. Estimates of elapsed thermal time from crop emergence (Tt) to the onset of tiller appearance for three canaryseed, one spring wheat and one oat cultivar seeded on three dates in 2013 and 2014.

Cultivar	Stat.An.[1]				Stat. An[4]					Stat. An.	
					SEM	Sign				SEM	Sign.
		2013					2014				
		Early	Late	V.Late			Early	Late	V.Late		
Togo		190	193	201[5]	16.8	ns[6]	196	194	194	7.4	ns
Bastia		158	200	181	20.5	ns	189	207	191	20.0	ns
Keet		171	161	190	16.1	ns	201	194	212	32.3	ns
Barrie		154	108	157*	5.7	*	146	187	113	13.5	+
Morrison		154	**104**	150*	4.7	*	177	202	**79*[5]**	7.7	*[6]
	SEM[2]	16.6	14.1	11.7			10.4	23.2	19.8		
	Sign.[3]	ns	*	+			+	ns	*		

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Statistical analysis for the seeding date means within a year × cultivar combination. [5] Seeding date means in bold differ significantly from the early seeding date mean within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a year × cultivar combination. Mean separations were conducted by Tukey' s tests. [6]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. Mean values and their separation are based on pooled observations of six plants replication^{-1} and two replications block^{-1}, thus only two blocks per year × cultivar have been used for the analysis.

Tt to the cessation of tillering ranged from 347 to 500, from 335 to 451, and from 335 to 411°Cd for canaryseed, wheat, and oat, respectively (Table 5.7). Differences in the Tt to the cessation of tillering between environments within years and cultivars were not significantly different. Only spring wheat and the canaryseed cultivar CDC Bastia had a lower Tt to the cessation of tillering for the late compared to the early SD, while the other cultivars had contrasting differences between environments within years.

Table 5.7. Estimates of elapsed thermal time from crop emergence (Tt), tiller number, average thermal time elapsed between the appearance of consecutive tillers and tiller appearance duration at the cessation of tiller appearance for three canaryseed, one spring wheat and one oat cultivar seeded on two dates in 2013 and 2014.

Cultivar	Stat.An.[1]			Sign[4].			Sign.
		2013			2014		
		Early	Late		Early	Late	
		Tt at the cessation of tiller appearance (°C d)					
Togo		421(29.9[5])a	389(0.0)ab	ns	493(32.3)a	500(117.0)a	ns
Bastia		476(62.1)a	425(35.6)ab	ns	465(56.0)a	394(65.6)a	ns
Keet		421(59.8)a	496(71.2)a	ns	493(32.3)a	347(39.9)a	*
Barrie		419(34.8)a	335(39.1)b	ns	451(0.0)a	398(55.2)a	ns
Morrison		411(51.9)a	335(39.1)b	ns	348(59.1)a	365(26.9)a	ns
	SEM[2]	46.0	33.4		35.7	38.6	
	Sign.[3]	ns	*		+	+	
		Tiller number at the cessation of tiller appearance					
Togo		3.1(0.52)a	2.4(0.26)ab	ns	3.1(0.11)ab	2.1(0.19)a	**
Bastia		2.0(0.45)a	2.6(0.37)ab	ns	2.5(0.06)b	1.8(0.21)a	*
Keet		2.6(0.24)a	3.7(0.72)a	ns	2.9(0.32)ab	1.6(0.60)a	ns
Barrie		2.9(0.38)a	2.4(0.23)ab	ns	3.3(0.09)a	3.0(0.67)a	ns
Morrison		1.9(0.23)a	1.6(0.25)b	ns	1.5(0.16)c	1.1(0.20)a	ns
	SEM	0.47	0.40		0.17	0.43	
	Sign.	ns	*		***	+	
		Average tiller appearance duration up to the cessation of tiller appearance (°Cd)					
Togo		232(31.5)a	196(1.6)b	ns	296(33.8)a	306(36.8)a	ns
Bastia		318(55.3)a	225(31.6)ab	ns	275(27.5)a	187(23.7)ab	+
Keet		250(33.6)a	335(29.6)a	ns	292(34.8)a	153(32.6)b	*
Barrie		265(34.8)a	227(39.3)ab	ns	305(13.1)a	211(46.2)ab	+
Morrison		257(51.8)a	230(39.2)ab	ns	172(59.1)a	162(28.0)ab	ns
	SEM	42.6	31.5		36.8	34.3	
	Sign.	ns	+		ns	*	
		Average elapsed Tt between the appearance of consecutive tillers up to the cessation of tiller appearance (°Cd)					
Togo		83(14.7)a	86(9.4)a	ns	98(12.8)a	144(14.2)a	+
Bastia		119(7.0)a	90(8.7)a	*	113(15.4)a	105(10.5)a	ns
Keet		96(8.0)a	99(16.4)a	ns	108(21.3)a	113(17.8)a	ns
Barrie		91(4.3)a	94(12.0)a	ns	94(4.1)a	72(10.8)a	ns
Morrison		138(21.8)a	141(15.7)a	ns	111(31.0)a	171(42.8)a	ns
	SEM[2]	13.3	12.8		19.2	22.7	
	Sign.[3]	+	+		ns	+	

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Statistical analysis for the seeding date means within a year × cultivar combination. [5] Seeding date means in bold differ significantly from the early seeding date mean within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [6]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.Mean values and their separation are based on the averages of two blocks environment^{-1}, four replications block^{-1} and six plants replication^{-1}.

Tiller number plant^{-1} at the cessation of tiller appearance ranged from 1.6 to 3.7, from 2.4 to 3.4, and from 1.1 to 1.9°Cd for canaryseed, wheat, and oat cultivars, respectively (Table 5.7). Differences among cultivars and between environments within years were generally non-significant. Average tiller appearance duration up to the cessation of tiller appearance ranged from 153 to 335, from 211 to 305, and from 162 to 257°Cd for canaryseed, wheat, and oat, respectively (Table 5.7). Any differences were attributed to the relatively large differences between environments within cultivars and years in the Tt to the cessation of tiller appearance and were generally better associated with tiller number relative to the average Tt elapsed between the appearance of consecutive tillers (Appendix 6).

Table 5.8. Maximum tiller number, tiller number at final harvest and tiller mortality (maximum tiller number minus that at final harvest) plant^{-1} for three canaryseed, one spring wheat and one oat cultivar seeded on two dates in 2013 and 2014.

Cultivar	Stat.An.[1]			Sign.[4]			Sign.
		2013			2014		
		Early	Late		Early	Late	
		Maximum tiller number plant^{-1}					
Togo		3.8(0.55[5])a	3.7(0.23)b	ns	3.7(0.18)ab	4.2(0.66)a	ns
Bastia		3.4(0.44)ab	4.0(0.34)b	ns	3.5(0.14)b	3.4(0.45)ab	ns
Keet		4.1(0.43)a	5.3(0.35)a	+	4.5(0.41)a	4.7(0.59)a	ns
Barrie		3.3(0.34)ab	3.2(0.22)bc	ns	3.8(0.14)ab	3.8(0.50)ab	ns
Morrison		2.1(0.15)b	2.2(0.15)c	ns	1.9(0.13)c	1.9(0.17)b	ns
	SEM[2]	0.55	0.28		0.23	0.47	
	Sign.[3]	**	***		***	**	
		Tiller number plant^{-1} at final harvest					
Togo		2.8(0.36)a	1.3(0.18)ab	*	1.9(0.21)a	1.6(0.14)b	ns
Bastia		2.2(0.08)ab	0.7(0.33)bc	*	1.7(0.40)a	2.4(0.38)a	ns
Keet		1.8(0.25)b	1.9(0.34)a	ns	1.3(0.43)ab	1.4(0.18)bc	ns
Barrie		1.4(0.29)bc	0.4(0.08)bc	*	1.2(0.17)ab	0.7(0.27)cd	ns
Morrison		0.6(0.11)c	0.1(0.05)c	**	0.2(0.04)b	0.5(0.08)d	*
	SEM	0.32	0.23		0.29	0.19	
	Sign.	***	***		*	***	
		Tiller mortality plant^{-1}					
Togo		1.1(0.34)a	2.4(0.24)ab	*	1.8(0.27)a	2.6(0.67)ab	ns
Bastia		1.2(0.39)a	3.2(0.23)ab	**	1.8(0.53)a	1.0(0.43)b	ns
Keet		2.3(0.23)a	3.4(0.43)a	+	3.2(0.71)a	3.3(0.31)a	ns
Barrie		1.9(0.29)a	2.8(0.22)ab	*	2.6(0.23)a	3.0(0.53)ab	ns
Morrison		1.5(0.17)a	2.1(0.16)b	*	1.7(0.12)a	1.5(0.21)ab	ns
	SEM	0.32	0.27		0.43	0.46	
	Sign.	+	*		ns	*	

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a response variable × year × seeding date combination. Cultivar means within a year × seeding date combination followed by the same letters do not differ significantly at 5% level. Mean separations conducted by Tukey's tests.[4] Statistical significance of test for the seeding date means within a year × cultivar combination. ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. [5] Numbers in brackets are standard errors. Mean values and their separation are based on two blocks per year × seeding date × cultivar, two replications block^{-1} and six plants replication^{-1}.

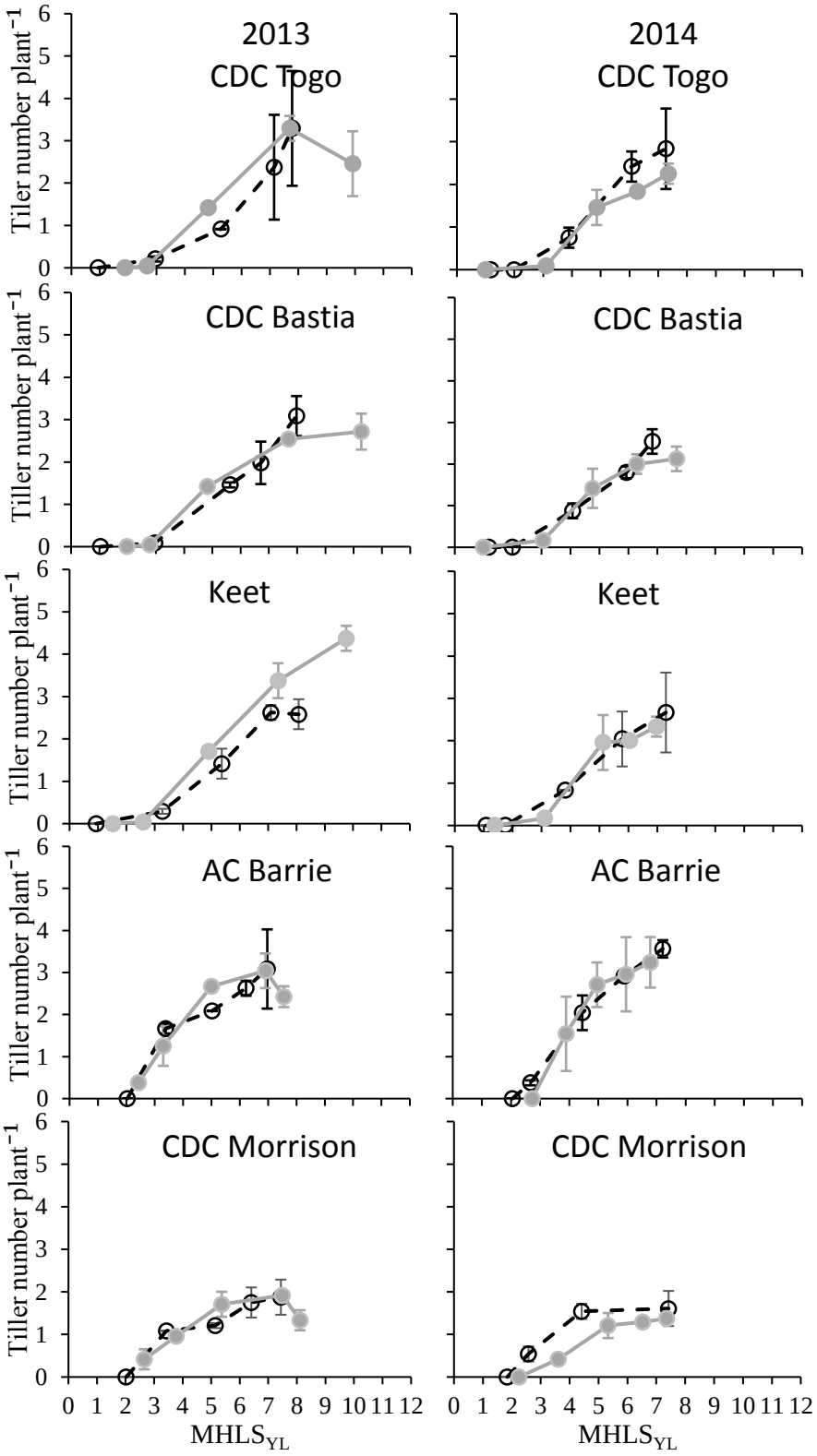

Figure 5.11. Tiller number plant^{-1} versus the modified Haun leaf stage ($MHLS_{YL}$) for three canaryseed, one spring wheat and one oat cultivar seeded early (empty symbols - black dashed line) and late (closed symbols - grey continuous line) in 2013 and 2014. Mean values are derived from observations conducted on two blocks seeding date^{-1}, two replications block^{-1} and six plants replication^{-1}. Symbols associated with data points represent standard error.

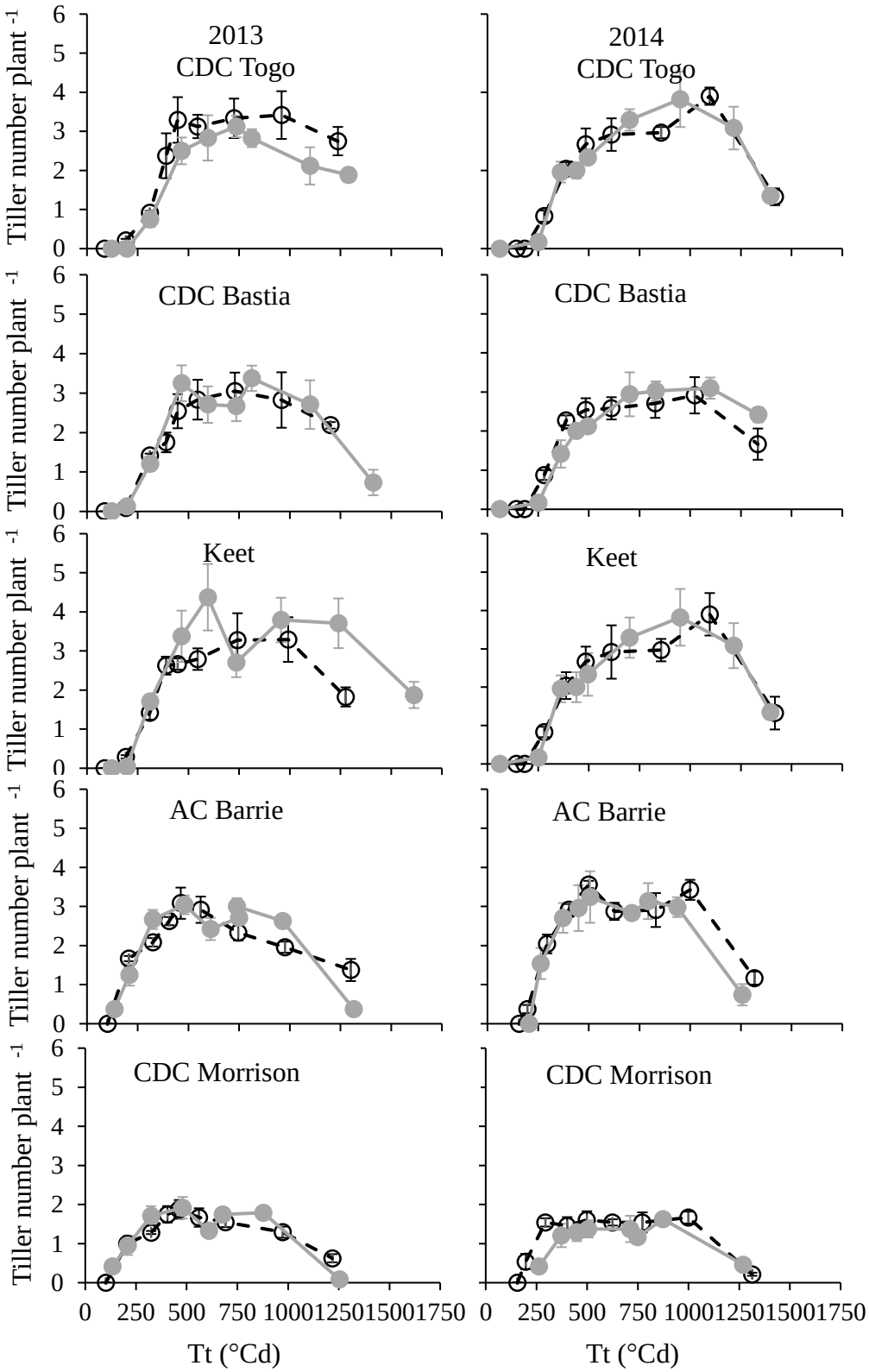

Figure 5.12. Tiller number plant^{-1} versus the thermal time from crop emergence (Tt) for three canaryseed, one spring wheat and one oat cultivar seeded early (empty symbols - black dashed line) and late (closed symbols - grey continuous line) in 2013 and 2014. Mean values are derived from observations conducted on two blocks seeding date^{-1}, two replications block^{-1} and six plants replication^{-1}. Symbols associated with data points represent standard error.

Cultivar differences in average elapsed Tt between the appearance of consecutive tillers up to tillering cessation within environments were statistically non-significant.

Maximum appeared tiller number ranged from 3.4 to 5.3, from 3.2 to 3.8, and from 1.9 to 2.2 for canaryseed, wheat, and oat, respectively (Table 5.8). Differences between SDs within years and cultivars were small and statistically non-significant.

In 2013, all crop cultivars but Keet had significantly ($P < 0.05$) reduced their tiller number at final harvest (Table 5.8) with late, relative to early SD. In 2014, however, the crop cultivars exhibited small and non-significant differences between SDs. The exception to that was oat, which had significantly ($P < 0.05$) increased tiller number at final harvest with late, compared to early SD. The cultivar responses were better explained by their response in tiller mortality than by their response in maximum tiller number (Appendix 7).

Cultivar effects on maximum tiller number and that at the final harvest within environments were significant ($P < 0.05$ but usually $P < 0.001$). Oat had the lowest values in all environments, and these were significantly ($P < 0.05$ but usually $P < 0.001$) lower relative to canaryseed.

5.3.3.2 Point of tiller appearance

Tillers formed at the coleoptile node (T0) of wheat and oat plants in most environments but the maximum percentage of plants on which T0 appeared was 29. (Table 5.9). Generally, primary tillers appeared on seedlings of all five crop cultivars. Tiller T1 appeared on a lower percentage of canaryseed plants compared to T2, independently of cultivar and SD. The only exception was the canaryseed cultivar CDC Bastia with the early seeding in 2013. In addition, greater differences in the percentages of tiller appearance between T1 and T2 were more common with later SDs for canaryseed. That was not the case for wheat and oat. Differences in tiller appearance percentages between T1 and T2 in wheat and oat were inconsistent between environments within years. Furthermore, T1 appeared on a higher percentage of plants compared to T2 with early- and late-seeded oat. The percentage of canaryseed plants on which primary tillers appeared decreased continuously from T3 to higher ranked tillers. The last primary tiller that appeared on canaryseed plants was either T3 or T4 as the percentage of plants on which T5 appeared was generally low. Secondary tillers appeared on canaryseed and wheat but not on oat plants. In canaryseed, more secondary tillers appeared with late, relative to early, SDs. The inversed was observed for wheat.

Table 5.9. Mean percentage[1] of plants that produced the coleoptilar tiller (T0) and the main stem tillers (T1-T5) and the secondary tiller numbers (T_{sec}) produced plant^{-1} for three canaryseed, one spring wheat and one oat cultivar seeded on two dates in 2013 and 2014.

	2013		2014	
Tiller description	Early	Late	Early	Late
	CDC Togo			
T0	0	0	0	0
T1	67	54	71	25
T2	83	92	88	92
T3	71	63	88	63
T4	58	13	29	4
T5	21	0	13	0
T_{sec} / plant	0.13	0.33	0.17	0.13
	CDC Bastia			
T0	0	0	0	0
T1	79	71	71	58
T2	58	88	83	79
T3	50	58	83	46
T4	67	29	17	21
T5	0	0	0	0
T_{sec} / plant	0.00	0.17	0.04	0.25
	Keet			
T0	0	0	0	4
T1	58	71	50	63
T2	83	100	92	100
T3	79	88	71	88
T4	38	67	46	38
T5	17	21	8	4
T_{sec} / plant	0.04	0.88	0.17	0.29
	AC Barrie			
T0	25	29	8	25
T1	88	83	63	83
T2	88	88	79	83
T3	50	4	79	67
T4	13	0	17	0
T5	0	0	4	0
T_{sec} / plant	0.29	0.25	0.38	0.25
	CDC Morrison			
T0	17	25	0	4
T1	83	71	63	54
T2	63	29	71	42
T3	4	4	17	29
T4	0	0	0	0
T5	0	0	0	0
T_{sec} / plant	0.00	0.04	0.04	0.08

[1] Percentages are derived from pooled observations on two blocks seeding date^{-1}, two replications block^{-1} and six plants replication^{-1}.

5.3.3.3 Start of stem elongation

Estimated elapsed Tt to the start of stem elongation ranged from 356 to 642, from 380 to 482, and from 386 to 462°Cd for canaryseed, wheat, and oat, respectively (Table 5.10). Stems of all three canaryseed cultivars began elongating significantly ($P < 0.01$) later, in terms of Tt, with late and/or very late, compared to early, SDs. Stems of wheat and oat cultivar also started elongating later, in terms of Tt, but the differences were significant ($P < 0.001$) in 2013 only.

The differences in Tt to the start of stem elongation between the early and the later SDs were greater for the canaryseed cultivars when compared to wheat and oat. This response was similar to that observed for FLN, as described in Table 5.2. In addition, the Tt to the start of stem elongation of canaryseed and wheat was associated with the FLN, whereas for oat, the relationship was weaker and significant at $P < 0.08$ (Figure 5.13). Tt to the start of stem elongation and FLN of canaryseed and wheat were positively and linearly associated, indicating that environmental conditions affecting the FLN on the mains stems of the plants have a direct positive effect on the Tt to the start of stem elongation (Figure 5.13).

Table 5.10. Estimates of the elapsed thermal time from crop emergence (Tt) to the start of stem elongation for three canaryseed, one spring wheat and one oat cultivar seeded on three dates in 2013 and 2014.

Cultivar	Stat.An.[1]				Stat. An[4]					Stat. An.	
					SEM	Sign				SEM	Sign.
		2013					2014				
		Early	Late	V.Late			Early	Late	V.Late		
		Tt at the start of stem elongation (°Cd)									
Togo		362	**475**	**552*[5]**	5.0	***[6]	440	**566**	**642***	10.5	***
Bastia		356	**465**	**519***	9.9	***	446	472	**538**	19.2	**
Keet		405	**537**	**573**	11.1	***	475	**592**	**622**	15.5	***
Barrie		380	**441**	**482***	5.1	***	430	463	463	17.0	ns
Morrison		386	**425**	**462***	6.0	***	402	439	433	23.6	ns
	SEM[2]	6.2	6.6	10.1			8.6	30.4	14.2		
	Sign.[3]	***	***	***			***	***			

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Statistical analysis for the seeding date means within a year × cultivar combination. [5] Seeding date means in bold differ significantly from the early seeding date mean within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [6]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.
Mean values and their separation are based on the averages of two blocks environment^{-1}, four replications block^{-1} and six plants replication^{-1}.

5.3.3.4 Cessation of tiller appearance

Estimated percentage of intercepted PAR (%IPAR) at the cessation of tillering ranged from 21 to 58, from 38 to 51, and from 37 to 45°Cd for canaryseed, wheat and oat, respectively (Figure 5.14). The slightly wider range in %IPAR of wheat compared to that of oat was due to the higher %IPAR values obtained with early versus late SDs in both years (Appendix 9). In contrast, for canaryseed cultivars, differences between SDs were not consistent across the years and higher for Keet and CDC Togo compared to CDC Bastia (Appendix 9). Tt at the cessation of tillering was significantly ($P \leq 0.0057$) and negatively linearly associated with the Tt to the start of stem elongation in CDC Bastia and Keet only (Figure 5.15).

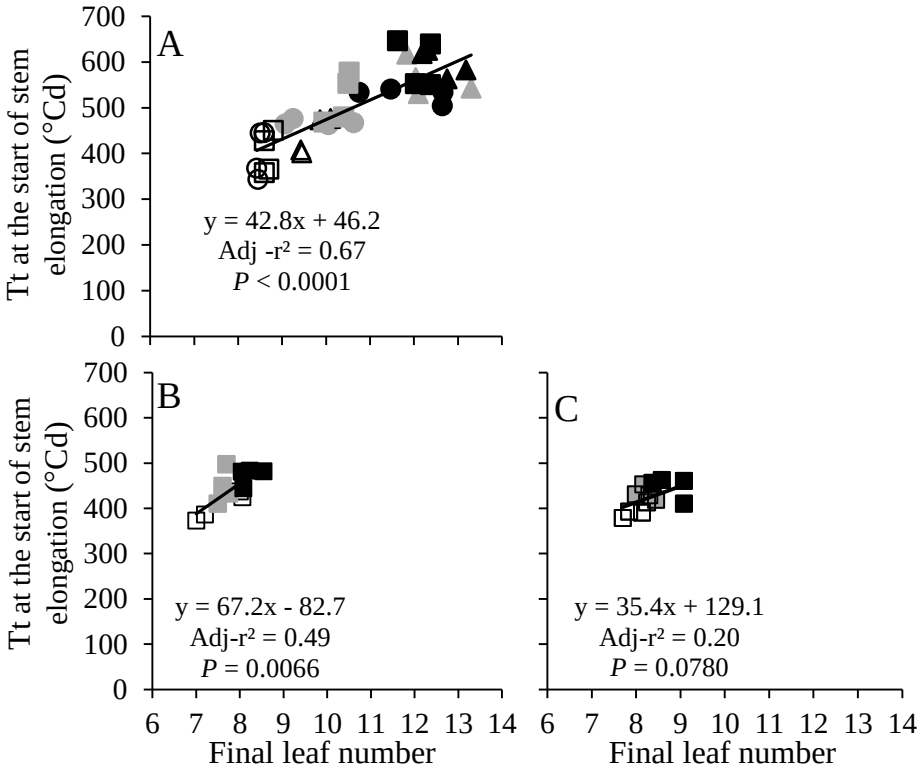

Figure 5.13. Thermal time (Tt) elapsed from crop emergence to the start of stem elongation versus the final leaf number on main stems for the canaryseed cultivars CDC Bastia (circles), Keet (triangles) and CDC Togo (squares) (A), wheat (B) and oat (C) seeded early (open symbols), late (grey-closed symbols) and very late (black-closed symbols) in 2013 and 2014. Data points represent means of one block, four replications block^{-1} and six plants replication^{-1}.

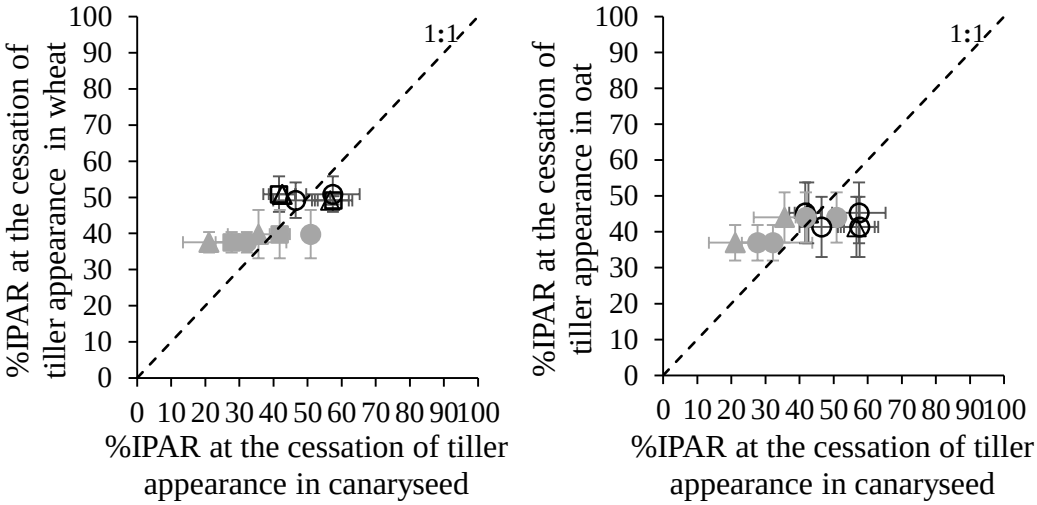

Figure 5.14. Comparison between the canaryseed cultivars CDC Bastia (circles), Keet (triangles) and CDC Togo (squares) and wheat (A) and oat (B) in the percentage of intercepted photosynthetically active radiation (%IPAR) at the cessation of tiller appearance when seeded early (open symbols) and late (closed symbols) in 2013 and 2014. Mean values are derived from observations on two replications block^{-1}. Symbols associated with data points represent standard error. Dashed line correspond to the 1:1 ratio.

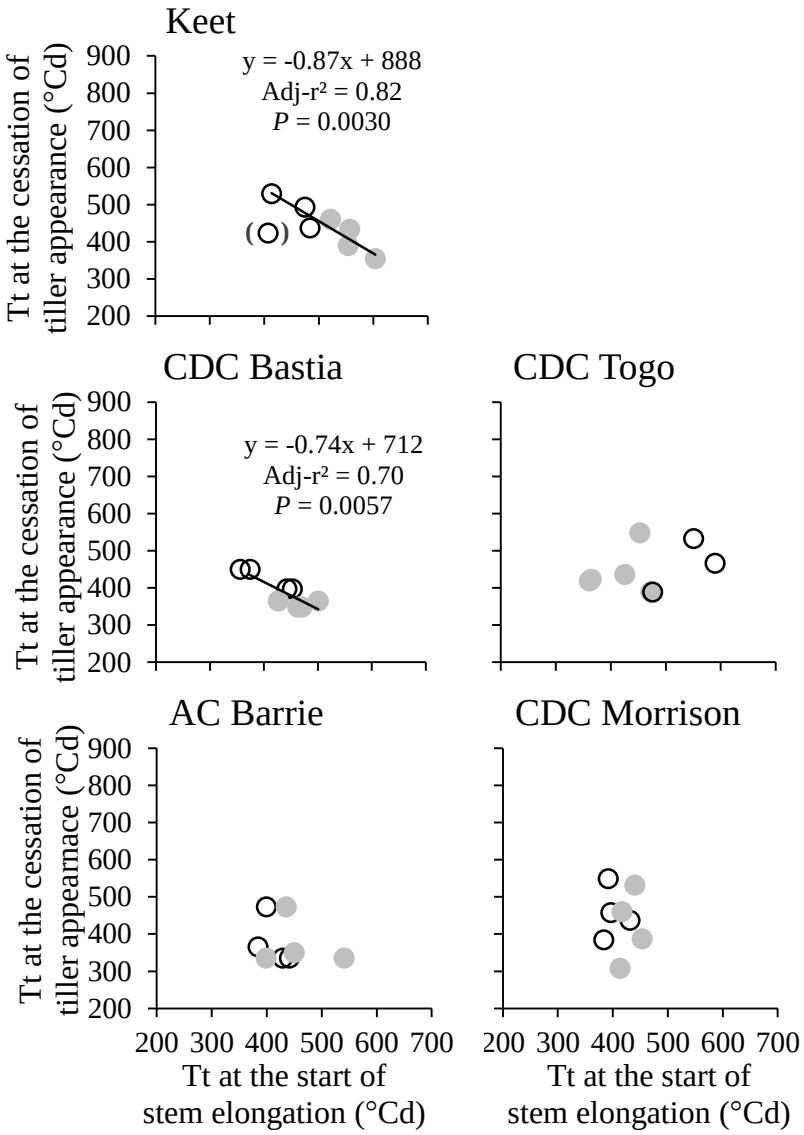

Figure 5.15. Thermal time elapsed from crop emergence (Tt) at the cessation of tiller appearance versus that at the start of stem elongation for canaryseed, spring wheat and oat cultivars sown early (open symbols) and late (closed grey symbols) in 2013 and 2014. Data points represent means of one block, two replications block^{-1} and six plants replication^{-1}. The data point in brackets was not included in the regression model.

5.4 Discussion

This present study investigated differences in leaf appearance and tillering among canaryseed, spring wheat and oat cultivars as related to seeding dates.

5.4.1 Leaf appearance

The relationship between the $MHLS_{YL}$ and Tt in all six environments was described by a bilinear function. The only exception was the early seeding in 2014 where the relationship was described by a trilinear function. The phyllochron, the inversed slope of the function (for early

seeding in 2014, see section *3.2.4 - phyllochron*), was estimated to be higher for the main stem leaves that appeared prior to the break point of the piecewise regression. Bilinear relationships between $MHLS_{YL}$ and Tt have also been reported for other cereals such as wheat (Calderini et al., 1996; Jamieson et al., 1995a; Miralles and Richards, 2000; Miralles et al., 2001; Steinfort et al., 2017) and barley (Kirby et al., 1982; Miralles and Richards, 2000; Miralles et al., 2001; Abeledo et al., 2004). However, in both those cereal crops, the change in the phyllochron was estimated to occur at higher ranked main stem leaves (ie, mainly between the fourth and the seventh leaf). The reported phyllochron pattern of wheat and barley is the opposite of that observed in canaryseed in all but one environment (early seeding in 2014). Main stem leaves that appeared prior to the break point had a lower phyllochron relative to those that appeared past the change. In contrast, a similar phyllochron pattern to that observed in canaryseed has been reported for rapeseed when sown on different dates (Miralles et al., 2001). The change in phyllochron of rapeseed plants was recorded between the ninth and the fifteenth leaf on plants that formed between 22 and 29 main stem leaves. That change in phyllochron was speculated to be related to the change in leaf morphology (ie, from petiolar to sessile shape). Similarly, the change in the phyllochron of canaryseed could be related to the very low individual leaf area of the first leaf (approximately 1 cm^2) relative to that of wheat and oat (approximately 3-4 cm^2), seeded at the same date. Specific leaf area index (leaf area over leaf dry mass) in early main stem leaves, which, in turn, was positively associated to embryo seed size, has been suggested by Lopez-Castaneda et al. (1996) to confer higher early vigor of barley and triticale in comparison to wheat and oat. The involvement of photosynthate availability and its positive effect on leaf initiation rate in dicots has been suggested by Savvides et al. (2014). A canaryseed seed weights approximately 7-8 mg, that is, about 20% of that of wheat and oat, and the resources that can be stored, are likely comparably low. In addition, canaryseed roots are thin and possibly less capable of exploring soil volumes compared to other species. Thus, it could be speculated that given the growth stage at which canaryseed phyllochron change occurs (between the first and the second leaf), it could be associated with seed and capture resources availability such as endosperm stored energy, radiation interception, and water and nutrient absorption.

To further speculate, the phyllochron change at the early growth stage of the plants could be related to the development of the plants in response to photoperiod. As explained earlier (sections 4.4.2.), canaryseed is likely a long day plant. Oat, canaryseed close relative, is also generally considered a long day plant (Sorrells and Simmons, 1992) with more diploid species (same ploidy level as canaryseed) and fewer tetraploid or hexaploid species exhibiting strong

photoperiodic response. This is because long day conditions considerably accelerate heading compared to short day conditions (Loskutov, 2001). When a long day plant from lower latitudes is exposed to long day conditions of higher latitudes, heading or anthesis can be hastened. Phyllochron, a basic component of phenological development of cereals, could possibly show lower values under the photoperiod conditions mentioned, in order for the plant to increase its development rate. Given that seedlings are able to respond to photoperiod once they expose their first leaf (or fraction thereof) to light energy, and given the leaf stage at which the phyllochron was estimated to have changed (1.1 to 1.5), it can be hypothesized that the phyllochron change in canaryseed is a response of plant phenology to long daylength.

The significant (P<0.001) differences of up to 12°Cd observed in the phyllochron of CDC Bastia with different SDs within years (Table 5.3) resulted in a maximum increase of 23% between SDs. These differences for CDC Bastia are smaller than these observed for the same cultivar by the repeated destructive harvests (31%) (Table 5.3). These differences are comparable to those observed for the other two canaryseed cultivars (23 and 18% for CDC Togo and Keet, respectively) and the oat cultivar (25%) but higher compared to those found for the wheat cultivar (11%). On the other hand, the differences reported for all five cultivars used in the study are smaller than those reported for wheat (36 and 53%) and barley (26 and 32%) cultivars (Miralles et al., 2001) and smaller than those reported for oat (41, 47 and 56%) cultivars (Sonego, 2000) across SDs. This might be related to the fact that both referenced studies were conducted at lower latitudes (34°S for results on wheat and barley and 43°S for oat,) where SDs exposed plants to a wider range of photoperiods.

The significant (P<0.001) differences observed in the FLN on main stem, the second basic component of cereal phenological development, exhibited a maximum increase of 38% across SDs. This finding will be the subject of a subsequent chapter of this thesis.

A phyllochron estimate of approximatelly 50 to 70°Cd calculated for canaryseed main stem leaves that appeared past the breakpoint of the piecewise regression between $MHLS_{YL}$ and the Tt in CDC Bastia, or that estimated destructively, is lower compared to an average over SDs estimate of 82-85°Cd for wheat (Miralles et al., 2001). It is also lower when compared to that of 85-110°Cd from a series of fertilizer application rate trials (Alzueta et al., 2012) for wheat cultivars and lower compared to an average over SDs estimate of 78-80°Cd (Miralles et al., 2001) and 96-120°Cd from a series of fertilizer application rate trials (Alzueta et al., 2012) for barley cultivars.

5.4.2 Tillering Pattern

5.4.2.1 Initiation of tillering

Tillering of CDC Bastia started after the appearance of the fourth main stem leaf (near 3.5 $MHLS_{YL}$ and before the fourth main stem leaf was fully expanded). Similarly, tillering in the other two canaryseed cultivars started near the same leaf stage as plants from the cultivar CDC Bastia, as illustrated in Figure 5.11. On the other hand, seedlings from both wheat and oat cultivars started tillering earlier, near the appearance of the third leaf due to the fact that tiller number $plant^{-1}$ was measured higher than zero in many treatments at or somewhat earlier than the full expansion of the third leaf (ie, third leaf stage). Similar results have been reported for spring wheat (Evers et al., 2006) and barley (Abeledo et al., 2004), both in water-stress free experimental plots. However, Hucl and Baker (1989) reported first tiller appearance (T0 or T1) at or slightly after the appearance of the fourth leaf for 10 wheat cultivars, seeded at 120 seeds m^{-2} (approximately half the seeding rate used in the present study) in a semiarid environment likely similar to that of the present study. Klepper et al. (1982) reported results in a winter wheat cultivar based on which T1 appeared around the appearance of the fourth leaf tip (third leaf stage) in a range of growing conditions. Under favorable conditions, when plants had experienced minimal stress from cold or drought, T0 appeared around the second leaf stage and T1 appeared when the third leaf was halfway emerged. Thereafter, one primary tiller appeared for approximately every elapsed phyllochron. Taking these results into consideration, along with the delay of about one leaf in canaryseed cultivars, relative to wheat and oat, for the appearance of their first primary tiller, and the higher phyllochron of their first main stem leaf compared to their later leaves, it appears that delayed leaf and tiller emergence might be associated in early canaryseed seedling development.

Delayed primary tiller appearance in canaryseed might also be associated with the suppression of T0 at all SDs, and the partial suppression of T1 as was observed with the late seeding of the cultivar CDC Bastia in both years of the study. T1 appeared on only half of the plants using non-destructive observations. Partial suppression of T1 was also recorded in all three canaryseed cultivars by the destructive harvesting. Such a finding has also been reported by Klepper et al. (1982) in winter wheat plants growing in dry, crusted and generally unfavorable seedbeds, such as those commonly found in the Canadian Prairies (Johnston et al., 2002), and likely more often with late-spring seeding. Klepper et al. (1982) speculated on a time "window" within which an axillary bud may begin to grow and once that "window" passes, the bud normally does not grow any further. Evers et al. (2006) discussed the assimilate source

to sink ratio of a plant, as it relates to tiller growth with a low ratio (ie, when the plant leaf area is relatively low), insufficient assimilates may be available and active axillary buds may not develop into tillers. The suppression of T0 and T1 in canaryseed cultivars might be related to their small seed size and the seedbed depths at seeding required to reach soil moisture. Hucl and Baker (1990) reported that increased seeding depth resulted in delayed and/or suppression of T0 and T1 in wheat.

5.4.2.2 Cessation of tillering and tiller number

Cessation of tillering in the canaryseed cultivar CDC Bastia occurred between the sixth and the eighth MS leaf stage (in situ observations). At that particular crop stage, the average (over four environments) %IPAR was estimated to be 49. Similar estimates of %IPAR were obtained for all three canaryseed from the destructively harvested seedlings. The corresponding values for wheat and oat cultivars (44 and 42, respectively) were similar, with narrower ranges compared to those measured for the canaryseed cultivars. Similar %IPAR values at the cessation of tiller bud growth have been suggested by Evers et al. (2006) and Alzueta et al. (2012) in spring wheat (ie, between 40 and 45). In barley, however, tiller appearance seems to continue beyond 40 %IPAR (Alzueta et al., 2012).

On the other hand, in two out of three canaryseed cultivars, namely CDC Bastia and Keet, Tt at tillering cessation was linearly and negatively associated with the start of stem elongation, when taking into account all environment × block data points except for one for Keet. In contrast, for the canaryseed cultivar CDC Togo, as well as in wheat and oat, the same two response variables were not associated. These findings indicate that under environmental and crop management conditions encountered during this study, the phenological phase of stem elongation in the canaryseed cultivars CDC Bastia and Keet, might be just as, or even more, important than %IPAR in the determination of the timing of tillering cessation.

Of interest in the relationship between the Tt at tillering cessation and the start of stem elongation in CDC Bastia and Keet, is the negative slope. That is, the later the stem elongation begins, the earlier the tillering cessation occurs. Such a finding cannot be explained by changes in the phyllochron and/or FLN as both response variables were higher (significantly or numerically) with late compared to early SDs. In the canaryseed cultivars CDC Bastia and Keet, a negative feedback mechanism could be involved in the regulation of tillering cessation. This is in contrast with what has been previously reported in wheat, where cessation of tiller appearance has been positively associated with stem elongation (Hay, 1999). In the present study, red to far-red ratio under the crop leaf canopy was not measured. However, the range of

%IPAR at tillering cessation in canaryseed was relatively wider, compared to wheat and oat and the relationships between the Tt at the tillering cessation and that at the start of stem elongation observed in CDC Bastia and Keet were significant (or near significant). These findings suggest that tillering cessation in canaryseed cultivars was more related to the onset of stem elongation and not to the important reductions in the available PAR levels associated with low red to far-red ratios under solar irradiance. This conclusion is supported by Casal et al., 1986, who suggested that low red to far-red ratio itself might preclude morphogenic responses to density before important depletion in energy availability occurs.

Given the tillering cessation response of the canaryseed cultivars CDC Bastia and Keet, with regards to the start of stem elongation, a lower tiller number at the cessation of tillering with late, compared to early, SDs would have been expected. Indeed, that was recorded in 2014, but not in 2013. This was due to the partial suppression of T1 and T2 in CDC Bastia and Keet, respectively, with the early, compared to the late, SD, which is even more clearly illustrated when data from all three SDs were considered (Appendix - Table 5A.4).

5.4.2.3 Tillering rate and duration

The average elapsed Tt between the appearance of consecutive tillers up to the cessation of tillering of 1.1 tillers 100°Cd^{-1} (averaged over years) recorded in wheat was a rate somewhat lower compared to that reported by Salvagiotti and Miralles (2007) (1.5 tillers 100°Cd^{-1}) for a well irrigated, short season cultivation in Argentina of a bread wheat cultivar, sown in containers and receiving basic nutrient solution. The average value of that elapsed Tt obtained in the current study is a comparable rate to that reported by Alzueta et al. (2012) in Argentina (ie, 1.2 tillers 100°Cd^{-1}) averaged over five wheat and three barley cultivars under similar agronomic practices. Differences in the average elapsed Tt between the appearance of consecutive tillers up to the cessation of tillering in temperate cereals have also been reported previsouly. Lopez-Castaneda et al. (1995) and Miralles and Richards (2000) reported higher tiller appearance rate emerged $leaf^{-1}$ and d^{-1}, respectively, for barley compared to wheat genotypes. In addition, the same two studies reported higher leaf appearance rates °Cd^{-1} and d^{-1}, respectively, and thus shorter phyllochron for barley compared to wheat cultivars. Given the coordination between leaf and tiller appearance in cereals (Klepper et al., 1982; Kirby et al., 1985), one might have expected that the higher leaf appearance rate, and thus shorter phyllochron, in canaryseed compared to wheat, would have been depicted in the differences between the two species in the average elapsed Tt between the appearance of consecutive tillers. In contrast, that Tt values observed in canaryseed were similar and slightly lower compared to

that observed for wheat and had a wider range (0.7 to 1.2 tillers 100^{-1} °Cd^{-1}). Such a response is likely related to the entire suppression of T0 and the suppression of T1 in most environments in canaryseed as illustrated by the percentages of plants on which those tillers appeared. The negative impact of the suppression of T0 and T1 tillers on the average elapsed Tt between the appearance of consecutive tillers in canaryseed was possibly partially compensated by the appearance of T4 or higher ranked primary tillers. The appearance of higher ranked primary tillers in canaryseed possibly increased the tillering duration and consequently increased the maximum tiller number in canaryseed, compared to oat, and often compared to wheat. However, in rain-fed, short-season crop production, late-formed tillers usually fail to reach physiological maturity. This was also apparent in the present study as tiller number at the final harvest was either nearly associated (in CDC Togo) or associated (in CDC Bastia and oat cultivars) with tiller mortality.

5.5 Conclusions

Canaryseed main stem leaf appearance rate changed during the expansion of the second leaf, while higher ranked leaves appeared faster compared to their preceding ones. Seed and capture resource availability and/or the prevailing photoperiod might be related to such a leaf appearance pattern. The average phyllochron of canaryseed appeared significantly higher with late compared to early (and/or very late) SDs and that was generally positively related to the number of tillers at the cessation of tiller appearance. In spite of the shorter phyllochron of canaryseed cultivars compared to wheat and oat, canaryseed tiller appearance rates were similar or even slightly lower than that of wheat due to the suppression of the first two or three primary tillers.

When environmental conditions in the present study favored higher FLN in canaryseed, this was accompanied by a delayed start of stem elongation. This in turn was associated with earlier cessation of tiller appearance, in terms of Tt. This was not the case in wheat and oat where the onset of tillering cessation was more closely related to the %IPAR. Canaryseed also exhibited a delayed onset of tiller appearance compared to wheat and oat, especially when seeded late. Canaryseed onset and cessation of tiller appearance may potentially shorten the tiller appearance duration, which, together with a potential suppression of primary tillers, determines the number of tillers with a higher probability of reaching physiological maturity.

Transition section between Chapter 5 and Chapter 6

Experiments in Chapter 5 investigated the leaf appearance and tillering pattern in canaryseed relative to spring wheat and oat in different growing environments to study a potential unmet vernalization requirement on determinants of time to anthesis (main stem leaf number, phyllochron and the onset and duration of stem elongation). Delayed seeding increased the main stem leaf number in canaryseed, relative to wheat and oat. In addition, it delayed the appearance of main stem leaves in canaryseed which was generally positively related to the number of tillers at the cessation of tiller appearance. Delayed seeding also delayed the onset of tillering and resulted in the suppression and earlier cessation of tillering in canaryseed, relative to wheat and oat. Cessation of tillering in canaryseed was negatively related to the start of stem elongation whereas in wheat and oat occurred within relatively narrow ranges of canopy light interception. Given the impact of unmet vernalization requirements on the adaptation of other small grain temperate cereals, the first two objectives of the experiments in Chapter 6 were to investigate the components of phasic development and the response of plant morphological characteristics closely related to grain yield. In light of the effect of delayed seeding on the number of tillers that reached physiological maturity, the contribution of tillers to grain yield in canaryseed was investigated. As in the previous two chapters, canaryseed responses are compared to those of wheat and oat.

Chapter 6 Differences among annual canarygrass, spring wheat and oat as related to seeding date in a semiarid environment: I. Plant phenology, morphology, growth and yield

6.1 Introduction

Canaryseed cultivars differed in their physiological age at key phenological stages and their final leaf numbers (FLNs) when seeded on different dates (Chapters 4 and 5). FLN in cereals usually closely relates to anthesis time (Hay and Kirby, 1991). While that may also be the case in canaryseed, time to anthesis was not studied in relation to FLN and phyllochron (the time required for a leaf lamina to unfold). On the other hand, Cogliatti et al. (2011) did find that crop cycle differences in terms of thermal time (Tt) among canaryseed accessions were principally related to those occurring from crop emergence to heading, but the authors did not study FLN and phyllochron.

Time to heading or anthesis largely determines crop adaptation and therefore grain yield in temperate environments (Richards, 1991) such as the Mediterranean-type environments and rainfed, short-season crop production systems, often encountered in the Canadian Prairies. The growing conditions encompass substantially increased temperature and increasingly lower soil water availability towards anthesis and different photoperiods at different crop phenological phases often accompanied by different integrals of incident solar radiation. Environmental factors such as temperature and photoperiod mainly determine the development of field crops (Slafer and Rawson, 1994). Other abiotic factors, such as water availability (eg, Estrada-Campuzano et al., 2008), nutrients (eg, Salvagiotti and Miralles, 2007), and light intensity and quality through plant population density (eg, Kirby and Faris, 1972), may determine crops development, but to a lesser extent compared to temperature and photoperiod. Miller (2000) and Bodega et al. (2003) reported delayed anthesis and maturity with delayed seeding. Furthermore, delayed seeding of canaryseed revealed a correlation (r=0.66**) between decreased yields and delayed heading for early- versus late-seeded canaryseed experimental plots (Hucl, personal communication, 2012). Therefore, it is reasonable to hypothesize that the phenological response of canaryseed cultivars to environmental factors might be associated with grain yield instability among site-years of cultivation. Information on phenological development of canaryseed has never been documented, so it is this study's first objective.

Segmentation of the whole or part of a cereal crop cycle to individual phenological phases has been practiced either for simulation modelling of crop development (Ritchie, 1991; Brown et al., 2013) or for crop breeding purposes (eg, Slafer et al., 2001). Such a practice has been

useful for many reasons (McMaster et al., 2005), including the examination of sensitivity of individual phases to environmental factors. For instance, the response of a low-temperature vernalization requirement of a vernalization-sensitive wheat genotype is confined to phenological phases prior to the floral initiation at the stem apex (Brown et al., 2013 and references therein). Similarly, the potential photoperiod sensitivity of wheat genotypes during the stem elongation phase has been suggested as a strategy to independently control the length of that specific development phase (Slafer and Rawson, 1994). Therefore, sequence examination of the phenological development of canaryseed cultivars might provide important information concerning the length of the individual phases. In addition, different genotypes might have different phenological responses under different environmental conditions when imposed by different seeding dates (SDs). Thus, determining these responses and their sequence for different cultivars is the second objective of this study.

FLN responses of canaryseed cultivars may theoretically increase photo-synthate production through increased leaf area and/or alterations in the stem elongation phase. In addition, FLN response could potentially alter the individual leaf area vertical profile in individual shoots, as Steinfort et al. (2017) showed in wheat. In that study, wheat isogenic lines with partially or unmet vernalization requirements had substantially lower flag-leaf area, related to short phyllochron, than those grown under short photoperiod and/or fulfilled vernalization requirement. If canaryseed plants reacted similarly, it would potentially affect the dry matter distribution between the inflorescence and the vegetative phytomers of individual shoots as it does in wheat (Gooding et al., 2000) and would likely affect the grain yield. Therefore, the study's third objective was to assess whether FLN response of canaryseed cultivars with different SDs alters key morphological characteristics and dry matter accumulation of canaryseed main stem closely related to the grain yield.

Evidence from studies on a single glabrous canaryseed cultivar (May et al., 2012a) suggest that early-seeded crops had more inflorescence-bearing tillers, which contributed disproportionally more to grain yield than the main stem inflorescences. Environmental factors that may affect tiller appearance and survival under rainfed conditions in the gramineous species are light intensity (for spring wheat, eg, Boss and Nueteboom, 1998; Evers et al., 2006), photoperiod (for spring wheat, oat and barley, eg, Peltonen-Sainio et al., 2009), temperature (for spring wheat, eg, Hucl and Baker, 1990; Boss and Nueteboom, 1998), nutrient availability (Prystupa et al., 2003; Alzueta et al., 2012), water availability (for wheat and triticale eg, Estrada-Campuzano et al., 2012) and the interactions of these factors with the genotype. Generally, long, inductive photoperiods at high latitudes or late SDs even at lower, non-extreme

latitudes have been reported to control the tillering pattern of temperate cereals by either depressing it due to shorter vegetative phases (Peltonen-Sainio et al., 2009; Steinfort et al., 2017) or enhancing it when vernalization and/or photoperiod requirements are not fulfilled and therefore vegetative phases are prolonged (Steinfort et al., 2017). Both of these responses decreased the contribution of tillers to grain yield because of either less tillering or high tiller mortality, respectively. Different site-years of cultivation and/or SDs, which have been reported to negatively affect canaryseed yield stability, may potentially alter one or more of the factors mentioned. Indeed, for late-seeded canaryseed, onset and cessation of tillering, with the latter being inversely correlated to the start of stem elongation, may potentially shorten the tiller appearance duration, which combined with a potential suppression of primary tillers determined the number of tillers which had a good chance of reaching physiological maturity (Chapter 5). Therefore, this study's fourth and last objective was to investigate the dry matter accumulation and importance of the contribution of tillers to canaryseed grain yield as affected by contrasting environmental conditions, mainly air temperature, by means of different SDs.

6.2 Materials Aand methods

6.2.1 Plant material

For information on the plant material used in this study see section 5.2.1.

6.2.2 Growing conditions

For years and location of the field experiments, soil type and chemical analysis, fertilizer application and weed control see section 3.2.2. For information on the average air temperature, cumulative rainfall and cumulative Tt refer to figure 3.1 and for information on the daylength see figure 4.1.

6.2.3 Experimental set-up

For information on the experimental design and the seeding practices see section 3.2.3. For plot organization see section 4.3.2.1.

6.2.4 Observations and estimates

For crop emergence estimation see section 5.2.4.

Observations from repeated destructive harvests were obtained in 2013 and 2014; all other observations were obtained in all three years.

Five types of measurements were conducted in 2013 and 2014 at different time intervals: i) every two to four days (ie, seedling stems dissections), ii) on a weekly basis (or 10-days

intervals if weather conditions did not allow for earlier sampling), iii) at mid- anthesis (hereafter referred to as anthesis), iv) post-anthesis {early milk development stage, Zadoks stage 73 (Zadoks et al., 1974)} and v) at physiological maturity. In 2012, phenological observations were carried out in situ on a weekly (or biweekly depending on the weather conditions) basis and destructive harvests were limited to the phenological stages of anthesis and physiological maturity. Destructive harvests for each SD within a year were conducted on different dates.

6.2.4.1 Observations conducted every two to four days

Dissections of seedlings stems:

In total, approximately 4000 seedlings were harvested and dissected from the 2013 and 2014 field experiments. In 2013, these seedlings were from the canaryseed cultivars CDC Togo, CDC Bastia and Keet. In 2014, only the latter two cultivars were used.

Estimates of the modified Haun leaf stage based on the youngest leaf ($MHLS_{YL}$, hereafter the abbreviation MHLS is used) at the FI and TS stages for the oat cultivar were obtained from model equations developed by Sonego et al. (2000). Estimates of MHLS at the TS and FI stages for the spring wheat were obtained from model equations described by Brown et al. (2013). Estimates of MHLS at the FI and TS stages for CDC Togo in 2014 were obtained from model equations developed from the 2013 and 2014 experiments (three SDs and two blocks per SD) as described in Appendices 13 and 14. For more information on seedling dissections refer to section 4.2.4.1.

6.2.4.2 Observations conducted on a weekly basis

Six seedlings randomly pre-selected and tagged for the purpose of detailed, on-plant-based observations were uprooted and partitioned into main stems and tillers and each of these two were further divided into leaf blades, stems (including leaf sheaths) and panicles/spikes later in the season for all three SDs in 2013 and 2014.

Plant Haun stage determination:

MHLS as described in Chapter 3 was applied up to the flag or penultimate leaf appearance for all the plots. Linear regressions between MHLS and the Tt from seeding for each experimental plot were conducted and the model equation was used to estimate the time at which the flag leaf was fully unfolded {the term flag leaf ligule (FLL) appearance is used} given the measured final number of leaves at anthesis. The slope of the linear model was used as an estimate of average phyllochron.

Plant organ growth and dry matter accumulation:

To determine dry matter accumulation, the plant samples were dried at 80^0C using an oven dryer (SB-550 Electric, The Grieve Corporation, IL, USA) for 48h, when stable dry weight was assumed to have been achieved (based on pilot tests done in 2012 on samples from a field experiment). The dry weights were recorded to the third decimal place. Periodical destructive observations of the main stem inflorescence dry matter accumulation were subjected to non-linear regression analysEs using a flexible sigmoid function for determinate growth:

$IDW = IDW_{max} * (1 + (Tt_e - Tt) / (Tt_e - Tt_m))*(Tt / Tt_e)^{(Tt_e / Tt_e - Tt_m)}$ (Equation 6.2)

(Yin et al., 2003), where IDW is the inflorescence dry weight and Tt is the thermal time after emergence. The model returns estimates of the Tt at which maximum growth rate was attained (Tt_m), maximum inflorescence dry weight (IDW_{max}) and the Tt at which IDW_{max} was reached (Tt_e). At Tte, the inflorescence growth terminated and was assumed to be the timing of grain filling cessation, which was used to calculate the main stem inflorescence grain filling duration by subtracting the Tt from emergence to anthesis. The grain filling duration in turn was used to calculate an average inflorescence filling rate as the quotient between the difference of the IDW at final harvest and anthesis over that. Given that the main stem inflorescence dry weight was measured only twice after anthesis (ie, a week to ten days after anthesis and at final harvest), the extra observation was assumed to have been taken a week after the observation of physiological maturity, while the IDW was set equal to that measured at final harvest. That assumption was required because of the difference between the two last measurements of the IDW, especially for wheat and oat cultivars, as Tte was usually overestimated.

Main stem height

Main stem height measurements were were conducted post-harvet by means of a ruller and subjected to non-linear regression analyses using the function

$SH = SH_{max} / (1 + e^{-k (Tt - Tt_m)})$ (Equation 6.3)

where SH is the stem height, SH_{max} is the maximum stem height, k is the maximum rate of change in stem height and Tt_m is the Tt at which k is achieved. Tt at $SH_{max1} = SH_{max} - 0.01* SH_{max}$ was also estimated using Equation 6.3 given that, at $SH = SH_{max}$, Tt tends to infinity and SH_{max1} is assumed to be equal to SH_{max}. Tt at the onset of stem elongation estimated in Chapter 5 was subtracted from the Tt after emergence and the Tt at stem elongation cessation was estimated. Stem elongation cessation in turn was used for the estimation of stem elongation duration and average stem elongation rate.

6.2.4.3 Observations conducted at anthesis (pollination)

The same destructive measurements, which were conducted on a weekly basis, were conducted at anthesis as well. Plots of each cultivar reached anthesis on different dates. The variability was higher for canaryseed, especially for late- and very-late-seeded plots, and therefore, the anthesis stage and harvest date was determined for individual plots. The six tagged plants of all five cultivars were not necessarily harvested on the same dates. If at least four out of six plants were at the anthesis stage while the remaining ones were close to that stage, then all six plants were harvested on the same date for the ease of the harvesting process. If the tagged plants were not close in terms of their development stage (especially for Keet), the plants were harvested on different dates. *In situ* stage determination of the individually tagged plants was regularly conducted around anthesis (three times a week) to determine the anthesis stage (Zadoks et al., 1974). Given that after the processes of pollination and fertilization the inflorescence becomes an important sink for carbohydrate partitioning and that this process occurs at different phenological stages for the three species used in this study, time of pollination was used as the criterion for anthesis determination. Time of pollination was determined based on the appearance of extruded anthers from florets located close to the middle of the panicle for canaryseed, few spikelets above and below the centre of the spike for wheat, and when the panicles were almost fully emerged for oat. Half-way pollination, therefore, was assumed at these phenological stages. The time of anthesis and FLN on the main stem was recorded for each of the six plants per plot and an average per plot was calculated. For FLN determination see section 4.2.4.1.

6.2.4.4 Observations conducted at post anthesis

The same destructive measurements that were conducted on a weekly basis were conducted at post- anthesis as well. Destructive harvests at this stage determined the main stem, tillers and main stem inflorescence dry matter accumulation. Therefore, the date of harvest was determined based on the anthesis date of each plot, the absence of anthers or presence of anthers which had ched their pollen at least on the plant main stem inflorescence and the attainment of maximum main stem height. Again, the plants were individually observed for the stage determination and the harvest practice was the same as for the anthesis stage.

6.2.4.5 Tt calculation at anthesis, post anthesis and physiological maturity

The daily accumulated Tt in degree-days was calculated as described in 3.2.4.2. Given that plants within a plot were not necessarily harvested on the same date, the average date of harvest

per plot was calculated using the Tt required for each single plant from crop emergence. When days after seeding or day of the year were needed, these were back-calculated from the relationship between the cumulated Tt and the day of the year that was described by a second-order polynomial function. In 2012 and 2014, Tt values deviated somewhat from the model function: the curve was split in four to six sub-curves whose model functions more accurately estimated day of the year.

6.2.4.6 Grain yield determination

At maturity, the inflorescences were individually hand-threshed and the grain was manually separated from chaff. Grain samples from individual inflorescences were de-hulled (wheat), partially de-hulled (canaryseed) or hulled (oat). Samples were oven-dried as described above.

6.2.5 Data Analysis

For data analysis refer to section 5.2.5.

6.3 Results

6.3.1 Phasic development from seeding to physiological maturity

Emergence of canaryseed seedlings of all cultivars across year × SD combinations (hereafter the term *environments* will be used) occurred five to twelve days after seeding. Seedlings of wheat and oat cultivars emerged a day earlier than canaryseed except from the very late SD in 2014, where the difference was approximately two days. The variability among environments in the time required from seeding to emergence was considerably lower when it was expressed in Tt (Table 6.1).

Canaryseed cultivars showed substantial variability in the Tt required from emergence to the stage of TS formation (Table 6.1). Although differences among SDs within year × cultivar combinations were inconsistent, very late seeded canaryseed required more heat units to reach to the TS stage. The range of such differences was from approximately 40°Cd (CDC Bastia in 2014) to 300°Cd (Keet in 2013). The corresponding ranges for wheat and oat cultivars were estimated to be from 14 to 100 and from zero to 90 °Cd, respectively. Differences in the Tt to TS stage among the three canaryseed cultivars within environments showed considerable variability especially with very late seeding, with Keet and CDC Bastia requiring the most and least Tt to reach to the TS stage, respectively. The cultivar order did not change between the two years. Differences between canaryseed cultivars and the other two species were present already with the early seeded crops, but they were not statistically significant. The differences

were significant ($P < 0.05$) with later SDs either due to the consistency in the Tt required by wheat and oat to achieve TS or due to their relatively smaller differences compared to canaryseed cultivars among within-years environments. The Tt from emergence to FI and FI to TS showed substantial and often significant ($P < 0.05$) differences among SDs within years for all three canaryseed cultivars. Generally, the Tt for each individual phase increased with later SDs (Table 6.1.). In contrast, the duration of the second phase for oats (ie, FI to TS) seemed consistent among environments. The Tt required for the canaryseed cultivars from emergence to TS was slightly better explained, as determined by the coefficient of determination, from the Tt required from FI to TS than from the time from emergence to FI (Appendix 11 – A and B).

The duration from emergence to TS in canaryseed correlated with that from emergence to FLL ($P < 0.0001$ - Appendix 11 - C). In contrast, the duration from TS to FLL was linearly related to the duration from emergence to FLL only for the early SDs (Appendix 11 - D).

The Tt requirement of the canaryseed cultivars from seeding to FLL was like the pattern described for the emergence to TS phase. However, the maximum difference among canaryseed cultivars across withi-year environments was approximately 325 °Cd, which was 1.5-fold and three-fold of the corresponding differences in wheat and oat, respectively. The Tt from seeding to FLL among environments for the canaryseed cultivars was significantly different ($P < 0.05$) and ranged from approximately 25 to 250 °Cd.

One of the two main components of the duration from seeding to FLL appearance, the FLN, showed a similar pattern to that of the Tt requirement of the treatments for that phase (Table 6.2). The FLN differences for each canaryseed cultivar across within-year environments were even more pronounced and always significant ($P < 0.05$). Although wheat and oat had higher FLN with later SDs relative to early SDs, the differences were not as large as those shown by the canaryseed cultivars. CDC Bastia and Keet had the smallest and largest changes in the FLN across within-year environments, respectively. The Tt duration from seeding to FLL appearance in canaryseed was significantly ($P < 0.0001$) associated with the FLN on the main stem (Figure. 6A.2 - A).

Unlike FLN, the other main component of the duration from seeding to FLL appearance, the average phyllochron, was not associated with the Tt duration of that phase (Appendix 12 - B). However, average phyllochron of canaryseed cultivars was generally significantly ($P < 0.001$) lower than that of the wheat and occasionally than that of oat (Table 6.2). Small differences among canaryseed cultivars within environments were not significant. Differences among canaryseed cultivar across within-year environments were generally significant ($P < 0.01$), with late SDs often resulting in higher estimates relative to early and/or very late SDs.

Table 6.1. Estimated elapsed thermal time (Tt) between seeding, emergence, floral initiation (FI), terminal spikelet (TS) and flag leaf ligule (FLL) appearance for three canaryseed, one spring wheat and one oat cultivars seeded on three dates in 2013 and 2014.

Cultivar	Stat.An.[1]				Stat. An[4]. SEM	Sign.				Stat. An. SEM	Sign.
		2013					2014				
		Early	Late	V.Late			Early	Late	V.Late		
		Tt from seeding to emergence (°Cd)									
Togo		119	107	105	-	-	113	87	108	-	-
Bastia		119	107	105	-	-	113	87	108	-	-
Keet		119	107	105	-	-	113	87	108	-	-
Barrie		104	94	82	-	-	99	76	76	-	-
Morrison		104	94	82	-	-	99	76	76	-	-
	SEM[2]	-	-	-			-	-	-		
	Sign.[3]	-	-	-			-	-	-		
		Tt from emergence to FI (°Cd)									
Togo		144a[4,5]	232ab	**305a**	13.9	*[6]	*210*ab[7]	*230*ab	***271*ab***	3.8	*
Bastia		162a	202b	**269a**	8.4	*	194b	212ab	262b	16.7	ns
Keet		155a	**259a**	**299a**	7.4	**	217ab	275a	**314a**	7.4	*
Barrie		*104*a	*145*c	***200*b**	9.8	*	*194*b	*157*b	*177*c	6.1	+
Morrison		*159*a	*186b*c	***254*ab*[5]	3.7	**	*232*a	*226*ab	*233*b	8.3	ns
	SEM	10.8	7.5	9.2			4.1	14.0	7.8		
	Sign.	+	**	**			*	*	**		
		Tt from FI to TS (°Cd)									
Togo		128a	-	197ab	25.7	ns	*104*a	***209*a**	***240*a***	3.6	**
Bastia		87a	259ab	181ab	24.4	+	94a	115bc	**170abc**	8.5	*
Keet		161a	**349a**	234a	18.6	*	142a	259a	216a	23.6	ns
Barrie		*145*a	*139*ab	*149*ab	14.2	ns	*139*a	*157*b	*151*bc	34.4	ns
Morrison		*105*a	*106*b	*98*b	2.8	ns	*94*a	*101*c	*101*b	5.3	ns
	SEM	14.8	31.1	19.2			13.2	8.3	13.1		
	Sign.	ns	*	*			ns	***	**		
		Tt from emergence to TS (°Cd)									
Togo		272a	-	502a	21.9	+	*313*a	***439*b**	***511*a***	5.7	**
Bastia		249a	461b	450ab	27.7	+	288a	327c	**432ab**	17.1	*
Keet		316a	**607a**	533a	20.5	*	359a	534a	531a	25.5	+
Barrie		*249*a	*291*c	***348*b**	8.1	*	*334*a	*314*c	*328*b	6.0	ns
Morrison		*264*a	***292*c**	***352*b***	1.2	***	*325*a	*327*c	*334*b	6.6	ns
	SEM	16.3	17.9	20.6			13.1	10.5	18.7		
	Sign.	ns	**	**			ns	***	**		
		Tt from TS to FLL appearance (°Cd)									
Togo		205a	-	227a	18.0	ns	258a	311a	240a	12.5	ns
Bastia		227a	194a	299a	29.3	ns	296a	315a	221a	22.9	ns
Keet		215a	166a	273a	29.9	ns	287a	249a	255a	28.0	ns
Barrie		*221*a	*244*a	*245*a	18.2	ns	*219*a	*270*a	*252*a	12.7	ns
Morrison		*244*a	*249*a	*188*a	10.5	+	*214*a	*172*a	*209*a	52.7	ns
	SEM	17.5	15.5	31.4			13.6	41.9	26.5		
	Sign.	ns	ns	ns			ns	ns	ns		

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Statistical analysis for the seeding date means within a year × cultivar combination. [5] Seeding date means in bold differ significantly from the early seeding date mean within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [6]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. [7] Means in italic are estimates obtained from model functions developed for the cultivar CDC Bastia as described in Section 6.2.4.1. and presented in the Appendices 13 and 14.

Table 6.2. Estimated elapsed thermal time (Tt) from seeding to main stem flag leaf ligule (FLL) appearance, final leaf number (FLN) and average phyllochron for three canaryseed, one spring wheat and one oat cultivar seeded on three dates in 2012, 2013 and 2014.

Cultivar	Stat. An.[1]				Stat. An.[4] SEM	Sign.				Stat. An. SEM	Sign.				Stat. An. SEM	Sign.
		2012					2013					2014				
		Early	Late	V.Late			Early	Late	V.Late			Early	Late	V.Late		
		Tt from seeding to FLL appearance (°Cd)														
Togo		756a	**645a**	**841b*[5]**	16.3	***[6]	595b	**754b**	**834b***	8.1	***	684bc	**836a**	**859a**	12.4	***
Bastia		753a	728a	810b****	16.8	*	595b	**761b**	**854ab***	10.2	***	697b	730b	**761b**	11.4	*
Keet		732a	685a	**925a***	26.2	***	650a	**880a**	**911a**	15.7	***	760a	870a	**893a**	36.3	*
Barrie		759a	739a	719c	12.2	+	574b	**629c**	**675c**	17.4	***	652bc	660b	656c	19.4	ns
Morrison		707a	705a	700c	18.9	ns	612ab	636c	622c	10.4	ns	638c	643b	619c	12.3	ns
	SEM	14.2	26.1	11.5			9.5	13.0	14.7			12.3	25.7	21.1		
	Sign.	+	ns	***			***	***	***			***	***	***		
		FLN														
Togo		8.1a	8.5a	**11.8b***	0.24	***	8.7b	**10.2b**	**12.2b***	0.13	***	8.7b	**10.5b**	**12.0a***	0.22	***
Bastia		8.1a	**10.2a**	**11.8b***	0.18	***	8.4b	**10.3b**	**12.6ab***	0.14	***	8.6bc	9.2c	**11.1b***	0.22	***
Keet		8.1a	**9.8a**	**13.3a***	0.34	***	9.4a	**12.7a**	**13.0a**	0.20	***	10.0a	**12.0a**	**12.6a**	0.22	***
Barrie		8.0a	**9.5a**	8.6c****	0.20	***	7.1d	**7.7d**	**8.5c***	0.08	***	8.0d	**7.6e**	8.1c****	0.10	**
Morrison		8.0a	**9.8a**	9.5c	0.45	*	7.8c	**8.2c**	**8.8c***	0.10	***	8.2cd	8.2d	**8.7c**	0.20	*
	SEM	0.14	0.41	0.22			0.10	0.3	0.17			0.13	0.13	0.36		
	Sign.	ns	ns	***			***	***	***			***	***	***		
		Average phyllochron (°Cd)														
Togo		78.6b	**49.9c**	**61.2c***	1.81	***	48.3b	**60.5b**	**53.4b***	0.86	***	56.2b	**69.3a**	57.9b****	1.35	***
Bastia		77.6b	**55.1c**	**57.8c**	2.65	***	52.4b	**61.1b**	53.6b****	1.24	***	60.7ab	**69.2a**	**52.7b***	2.09	***
Keet		75.0b	**52.0c**	**61.1c***	1.86	***	53.0b	57.6b	57.3b	1.65	ns	56.5b	**66.4a**	59.7b****	1.84	**
Barrie		91.5a	**73.7a**	85.6a****	2.03	***	72.5a	77.6a	73.7a	2.47	ns	67.1a	75.6a	75.2a	2.98	ns
Morrison		78.8b	**63.8b**	**70.7b***	1.44	***	70.2a	72.6a	**57.2b***	1.83	***	59.9b	66.8a	59.7b	3.18	+
	SEM[2]	3.20	1.98	1.38			1.27	1.95	2.19			1.71	2.76	2.58		
	Sign.[3]	***	***	***			***	***	***			***	ns	***		

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Statistical analysis for the seeding date means within a year × cultivar combination. [5] Seeding date means in bold differ significantly from the early seeding date mean within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [6]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤ 0.1, ≤0.05, ≤0.01 and ≤0.001.

For canaryseed, the duration from emergence to TS, and not that from TS to anthesis, was associated with the duration from emergence to anthesis (Figure 6.1 – A and B). The differences between the early and later SDs in Tt from emergence to TS were depicted in the differences between early and later SDs in Tt from emergence to anthesis (Figure 6.2.).

In canaryseed, the longer duration from emergence to TS was negatively associated with the stem elongation phase (TS to anthesis) which may partly explain why only 64% of the variation in the relationship in Figure 6.2 was explained (Appendix 12 – C). This is also evidenced by the duration in Tt from FLL appearance to anthesis (Table 6.2). With the exception of the 2012 data, later SDs had a reduced duration from FLL appearance to anthesis for all three canaryseed cultivars. Differences among canaryseed cultivars or between canaryseed cultivars and the other two species within environments were generally not significant.

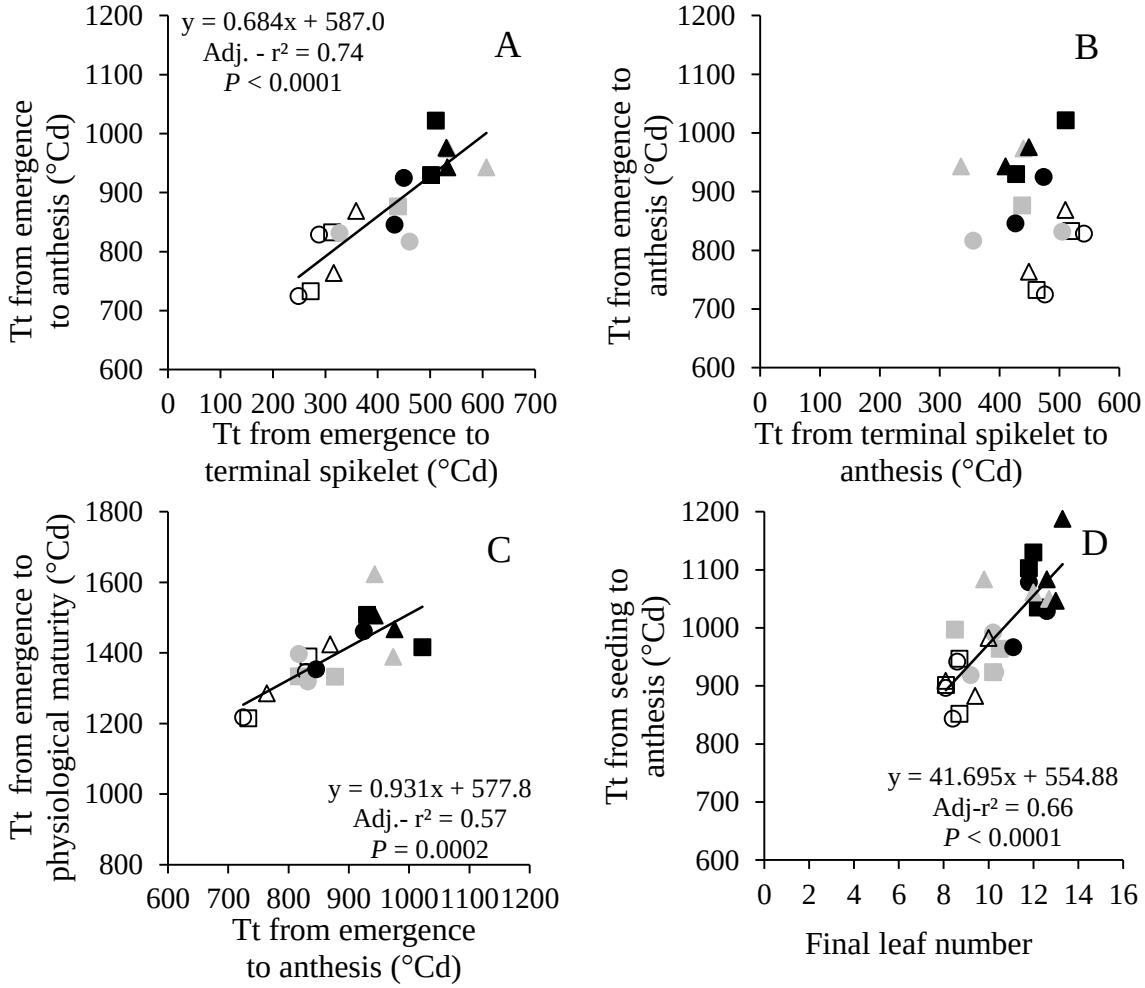

Figure 6.1. Thermal time (Tt) elapsed from crop emergence to terminal spikelet (A); and from terminal spikelet to anthesis (B) versus the Tt from emergence to anthesis; Tt elapsed from crop emergence to anthesis versus the Tt from crop emergence to main stem physiological maturity (C) and Tt from seeding to anthesis versus the final leaf number on plant main stem (D) for the canaryseed cultivars CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) seeded early (empty symbols), late (grey-closed symbols) and very late (black-closed symbols) in 2013 and 2014.

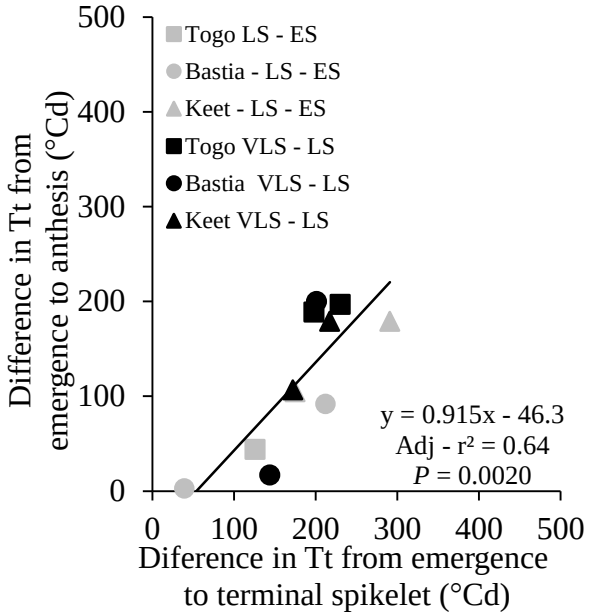

Figure 6.2. Differences between early and later seeding dates in Tt from crop emergence to anthesis versus the difference between early and later seeding dates in Tt from emergence to terminal spikelet. Letters ES, LS and VLS following the cultivars names in the figure legend denote the seeding date and stand for early, late and very late seeding date, respectively.

In general, the Tt duration from seeding or emergence to anthesis was significantly ($P < 0.05$) increased with later SDs for all three canaryseed cultivars (Table 6.3). The maximum difference among SDs within a year was 200 °Cd. In contrast, the duration from seeding to anthesis for wheat and oat cultivars was consistent or increased up to 70 °Cd. Canaryseed cultivars showed differences in the duration from seeding to anthesis. Duration from seeding to anthesis for Keet was highest when seeding was delayed from early to late, but for CDC Bastia when seeding was delayed from late to very late. CDC Togo showed an intermediate response.

The duration from emergence to anthesis was associated with the total main stem cycle (until physiological maturity) for all canaryseed cultivars when considering all environments. However, despite the relationship's high significance level ($P = 0.0020$), only approximately half of the variation of main stem cycle was explained by the duration from emergence to anthesis. Few data points from late and very late seeding fell far off the linear relationship (Figure 6.1 - C), likely because of the duration in Tt from anthesis to main stem physiological maturity, which was inconsistent among environments for all three canaryseed cultivars. Although wheat and oat showed differences of up to 60 °Cd in their duration from anthesis to main stem physiological maturity, the corresponding differences for canaryseed cultivars were as high as 160 °Cd (Table 6.3).

Table 6.3. Estimated elapsed thermal time (Tt) between seeding, flag leaf ligule (FLL) appearance, main stem anthesis and main stem physiological maturity for three canaryseed, one spring wheat and one oat cultivar seeded on three seeding dates in 2012, 2013 and 2014.

Cultivar	Stat. An.[1]				Stat. An.[4]					Stat. An.				Stat. An.	
					SEM	Sign.				SEM	Sign.			SEM	Sign.
		2012					2013					2014				
		Early	Late	V.Late			Early	Late	V.Late			Early	Late	V.Late		
		Tt from FLL appearance to main stem anthesis (°Cd)														
Togo		146a[1]	**349ab**	**251ab*[5]**	15.6	***[6]	257ab	**170ab**	**201ab**	12.5	***	262ab	**128a**	271a*	18.2	***
Bastia		145a	**261bc**	**261ab**	17.2	***	248ab	**163ab**	**175ab**	15.0	***	245ab	**190a**	207ab	14.1	*
Keet		177a	**398a**	**286a***	30.8	***	233b	170ab	**136b**	19.7	**	223b	191a	158b	30.0	ns
Barrie		140a	166c	**236b***	14.1	***	276a	**204a**	**228a**	14.5	**	277a	209a	232ab	19.6	+
Morrison		174a	157c	140c	19.1	ns	184c	**128b**	213a*	14.1	***	234ab	**183a**	214ab	12.1	*
	SEM[2]	16.5	26.9	12.0			10.6	14.3	17.6			12.6	24.6	22.3		
	Sign.[3]	ns	***	***			***	***	**			*	ns	**		
		Tt from anthesis to main stem physiological maturity (°Cd)														
Togo		-	-	-	-	-	482b	**552b**	**578a**	14.9	***	557a	**457bc**	**395c***	15.4	***
Bastia		-	-	-	-	-	494b	**580b**	538a	25.0	**	518ab	487ab	494b	14.6	ns
Keet		-	-	-	-	-	523ab	**680a**	563a*	20.2	***	556a	**415c**	490b*	18.9	***
Barrie		-	-	-	-	-	555a	577b	538a	18.0	ns	487b	465abc	505ab*	10.5	*
Morrison		-	-	-	-	-	524ab	**585b**	**574a**	8.1	***	541a	521a	566a*	15.9	*
	SEM	-	-	-	-	-	11.1	22.9	15.4			9.9	18.8	17.3		
	Sign.	-	-	-	-	-	***	**	ns			***	***	***		
		Tt from seeding to main stem anthesis (°C d)														
Togo		902ab	**997b**	**1103b***	62	***	852ab	**924b**	**1035a***	8.2	***	947b	964b	**1130a**	16.7	***
Bastia		897b	**992b**	**1079b***	3.7	***	844b	**924b**	**1029a***	14.6	***	942b	919c	967b*	10.1	*
Keet		909a	**1084a**	**1188a***	15.9	***	883a	**1050a**	**1047a**	12.4	***	983a	**1061a**	**1084a**	16.5	**
Barrie		899ab	905c	**955c**	4.0	***	850b	**833c**	**903b***	4.4	***	929b	**869d**	**888c**	6.4	***
Morrison		881c	**860d**	**840d***	5.9	***	796c	**763d**	**835c***	6.0	***	872c	**825e**	**833c**	2.5	***
	SEM	3.8	6.1	14.2			7.5	5.6	11.3			7.8	10.5	19.5		
	Sign.	***	***	***			***	***	***			***	***	***		
		Tt from seeding to main stem physiological maturity (°C d)														
Togo		-	-	-	-	-	1334b	**1478bc**	**1613a***	12.8	***	1503a	**1420b**	1524a*	16.2	***
Bastia		-	-	-	-	-	1337b	**1504b**	**1567a***	13.9	***	1460b	**1406b**	1462b*	12.1	**
Keet		-	-	-	-	-	1405a	**1730a**	**1610a***	16.4	***	1539a	**1476a**	**1574a***	9.1	***
Barrie		-	-	-	-	-	1405a	1409cd	1440b	20.3	ns	1416c	**1335c**	1394c*	8.8	***
Morrison		-	-	-	-	-	1320b	1348d	**1409b***	9.3	***	1413c	**1346c**	1398c*	14.7	***
	SEM	-	-	-	-	-	10.4	20.2	12.5			9.1	11.6	14.4		
	Sign.	-	-	-	-	-	***	***	***			***	***	***		

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Statistical analysis for the seeding date means within a year × cultivar combination. [5] Seeding date means in bold differ significantly from the early seeding date mean within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [6]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.

6.3.2 Plant morphological characteristics and dry matter accumulation

6.3.2.1 Individual leaf area

When canaryseed was seeded early, main stem penultimate and flag leaf areas were smaller than those of their preceding leaves (Figure 6.3). A similar pattern was found for the late SD when the areas of the three or four top main stem leaves were smaller than those of the preceding leaves. Flag leaf and occasionally penultimate leaf areas in both wheat and oat cultivars were also smaller compared to those of their preceding leaves, but the effect of SD on the pattern of individual leaf areas of the top five phytomers was not consistent across years. Flag leaf and penultimate leaf areas with early SDs were significantly ($P < 0.05$) higher compared to that with late SD in all three years in Keet but less frequently in CDC Togo and CDC Bastia (Figure 6.3). Significant ($P < 0.05$) differences among SDs in flag leaf and penultimate leaf areas were also present in the other two species but the pattern was not consistent across years.

Despite the significantly ($P < 0.05$) smaller flag leaf area for the late- compared to the early-seeded trials in five out of nine year × canaryseed cultivar combinations, there was no significant correlation between FLN and flag leaf area (Figure 6.4-A). That was also true for the oat cultivar (Figure 6.4-B). However, FLN and flag leaf area were significantly ($P < 0.001$) and positively correlated in wheat (Figure 6.4-C). The main stem grain yield of canaryseed significantly and positively correlated with flag leaf area for the early SD (Figure 6.5-A) but no correlation was found for wheat and oat (Figure 6.5-B and C).

6.3.2.2 Main stem elongation and height

Main stem height data fitting with the logistic function returned estimates of its maximum height, its maximum elongation rate, Tt elapsed from emergence to when that rate was achieved and to the stem elongation cessation (Tt_e) (n=7, Adj-r^2 ≥0.93 but most of the values were equal to or higher than 0.98, $P < 0.0001$).

Late-seeded wheat and oat plants had significantly ($P < 0.05$) shorter main stems than early-seeded plants in both 2013 and 2014. That trend was also true for the canaryseed cultivars but the differences between the SDs were smaller than those found for wheat and oat and significant ($P < 0.05$) only in 2014 (Table 6.4). CDC Bastia had the shortest maximum main stem height (reffered to as stem height hereafter) and had the largest reduction among canaryseed cultivars with late, relative to early, SD in both years.

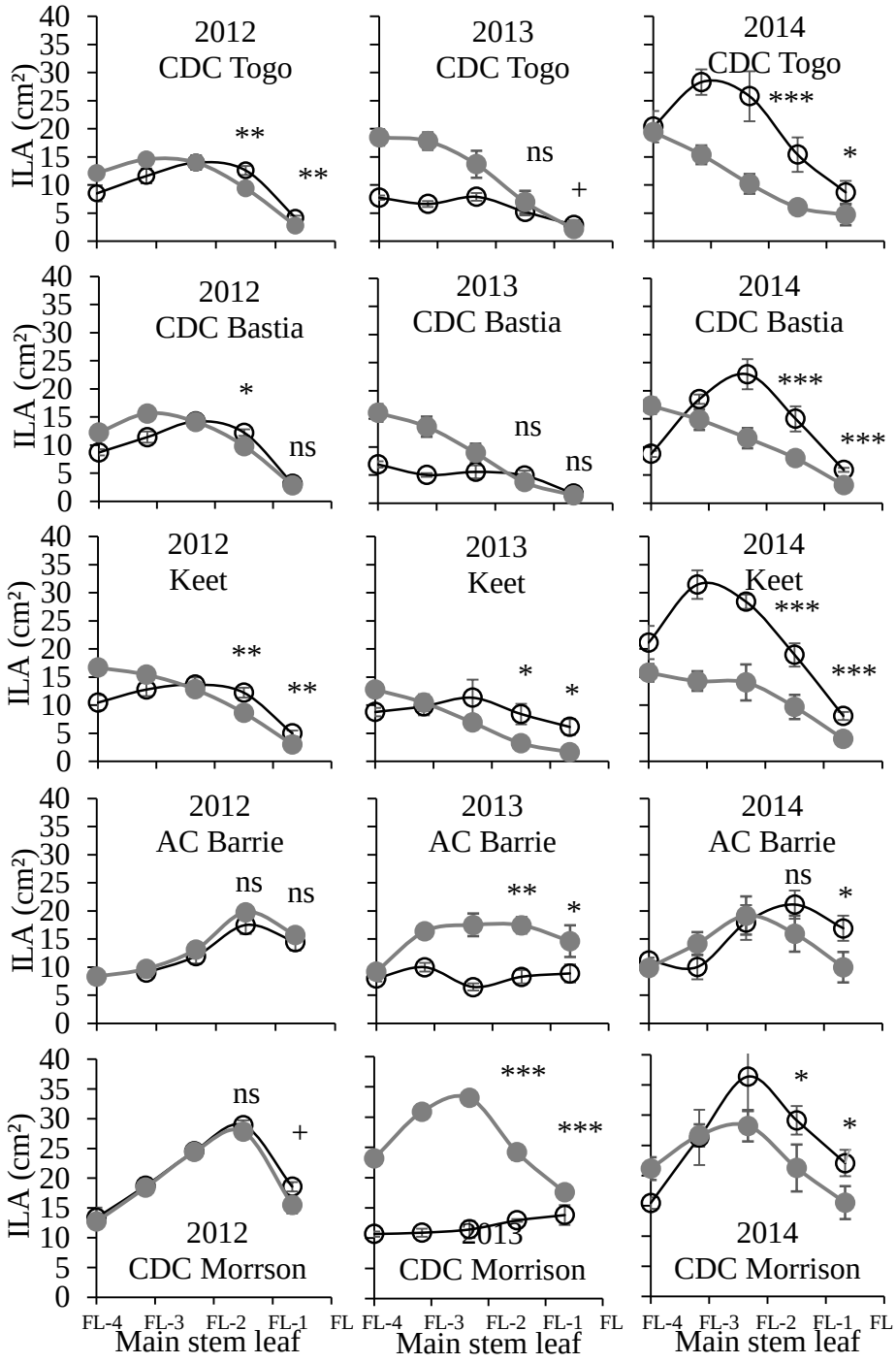

Figure 6.3. Individual leaf area (ILA) of the top five main stem phytomers for three canaryseed, one spring wheat and one oat cultivar when seeded early (open symbols - thin black line) and late (grey-closed symbols - grey line) in 2012, 2013 and 2014. FL on X-axis stands for 'flag leaf'. FL-1 denotes the penultimate leaf, FL-2 the second leaf below the flag leaf and so on. Vertical bars represent standard error when larger than symbols. Statistical analyses by year and cultivar were conducted for the penultimate and flag leaf only. ns, +, *, ** and *** used to denote that the statistical significance within a year × cultivar combination is >0.1, <0.1, <0.05, <0.01 and <0.001.

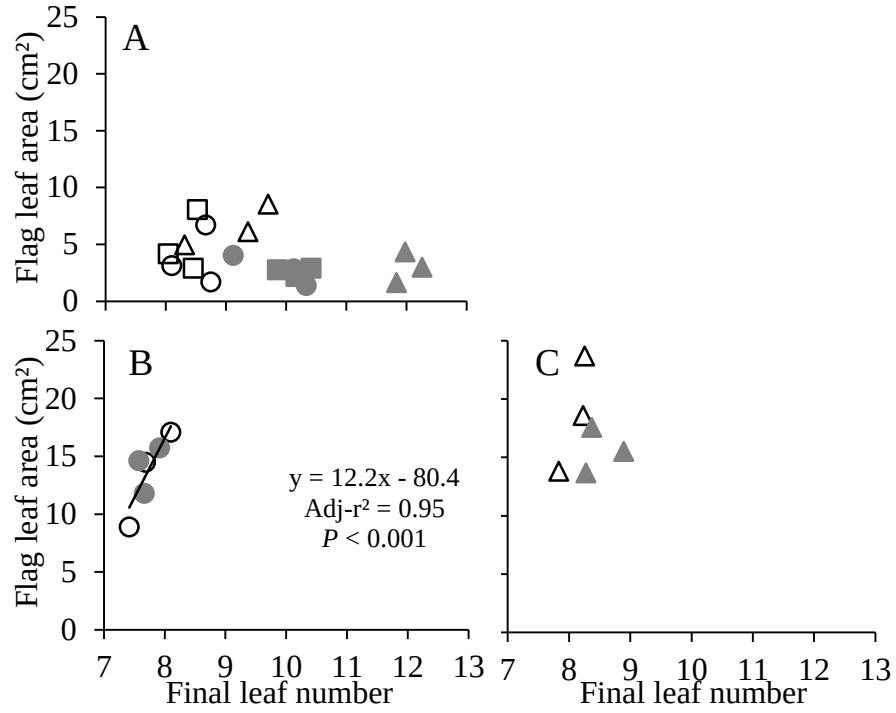

Figure 6.4. Flag leaf area versus final leaf number for the canaryseed cultivars CDC Bastia (circles), Keet (triangles) and CDC Togo (squares) (A), the spring wheat cultivar (B) and the oat cultivar (C) when seeded early (open symbols) and late (grey closed symbols) in 2012, 2013 and 2014.

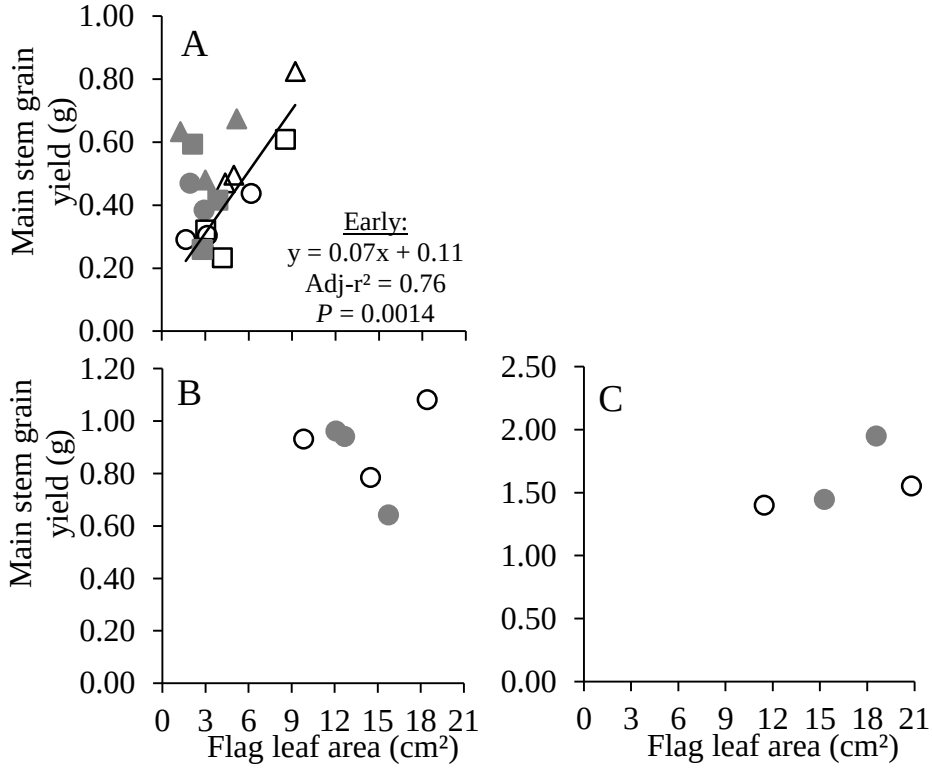

Figure 6.5. Main stem grain yield versus flag leaf area for the canaryseed cultivars CDC Bastia (circles), Keet (triangles) and CDC Togo (squares) (A), the spring wheat cultivar (B) and the oat cultivar (C) when seeded early (open symbols) and late (grey-closed symbols) in 2012, 2013 and 2014. Main stem grain yield of oat in 2012 was not recorded.

Table 6.4. Estimates of elapsed thermal time from crop emergence to when maximum main stem elongation rate was achieved (Tt_m), to anthesis (Tt_{Em-An}) and to stem elongation cessation (Tt_{SEC}), thermal time of main stem elongation duration (Tt_{SED}), maximum main stem height (SH_{max}) and average main stem elongation rate (ASER) for three canaryseed, one spring wheat and one oat cultivar seeded on two dates in 2013 and 2014.

Year	Cultivar	Seeding date	Estimates					
			Tt_m (°Cd)	Tt_{Em_An} (°Cd)	Tt_{SEC} (°Cd)	Tt_{SED} (°Cd)	SH_{max} (cm)	ASER (cm °Cd^{-1})
2013	Togo	Early	605	738	1039	677	93.8	0.200
		Late	713	813	1047	572	90.7	0.208
		P-value[1]	***	***	ns	**	ns	ns
	Bastia	Early	580	733	939	583	88.4	0.207
		Late	685	813	1032	572	84.1	0.214
		P-value	***	***	*	ns	ns	ns
	Keet	Early	648	777	1054	649	98.6	0.228
		Late	820	948	1240	697	98.5	0.195
		P-value	***	**	*	ns	ns	*
	Barrie	Early	570	748	841	461	83.9	0.226
		Late	603	739	860	419	73.6	0.235
		P-value	*	ns	ns	ns	*	ns
	Morrison	Early	601	683	955	569	78.1	0.191
		Late	641	669	969	544	70.0	0.151
		P-value	*	ns	ns	ns	**	**
		$SEM^{E, 2}$	8.8	13.2	25.9	26.5	1.90	0.0082
		P-value	***	**	***	***	***	*
		SEM^{L},	9.3	8.3	43.0	49.1	2.34	0.0055
		P-value	***	***	***	**	***	***
2014	Togo	Early	746	836	1287	847	97.4	0.190
		Late	815	878	1271	705	95.0	0.251
		P-value	*	*	ns	+	ns	*
	Bastia	Early	678	843	1057	612	94.7	0.231
		Late	720	830	982	502	82.2	0.223
		P-value	+	+	ns	+	***	ns
	Keet	Early	774	854	1321	846	107.6	0.200
		Late	871	1002	1282	694	101.9	0.221
		P-value	*	***	ns	ns	*	ns
	Barrie	Early	665	825	1028	597	94.5	0.221
		Late	696	781	863	432	70.1	0.225
		P-value	*	**	**	**	***	ns
	Morrison	Early	665	773	1125	723	82.0	0.179
		Late	730	754	968	531	65.3	0.155
		P-value	***	*	*	+	**	ns
		SEM^{E}	12.9	5.8	35.6	37.8	2.13	0.0074
		P-value	***	***	***	***	***	**
		SEM^{L},	18.7	12.6	62.2	66.8	2.48	0.0272
		P-value	***	***	***	*	***	ns

[1]ns, +, *, ** and *** used to denote that the statistical significance of the difference of the means within a year × seeding date and a year × cultivar combination is >0.1, <0.1, <0.05, <0.01, and <0.001.
[2]SEM stands for Standard Error of Mean and superscripts E and L are used to denote the SEM which may be used for cultivar means comparison within early and late seeding date within each year, respectively.

Stem height of canaryseed cultivars significantly ($P = 0.0183$) and positively correlated with the Tt from crop emergence to anthesis for late-seeded crops (Figure 6.6-A). That was due to the positive linear association with its elongation duration while no significant relationship was found with its average elongation rate (Figure 6.6-C and B, respectively). Average stem

elongation rate was not significantly different between the SDs for both glabrous canaryseed cultivars and the wheat cultivar but was either numerically or significantly ($P < 0.01$) lower with late- relative to early-seeded oat (Table 6.4). The stem elongation duration, in turn, was usually longer for early versus late-seeded crops of all five cultivars and significantly ($P < 0.001$) shorter for wheat and oat compared to canaryseed. In addition, the main stem elongation duration of late-seeded canaryseed plants was significantly ($P = 0.016$), positively and linearly associated with FLN which, in turn, was significantly ($P = 0.041$), positively and linearly associated with stem height (Figure 6.6-E and D, respectively).

6.3.2.3 Main stem inflorescence growth and filling characteristics

Main stem inflorescence dry weight data fitted to the Beta-growth function provided estimates of the Tt elapsed from emergence to main stem inflorescence growth cessation and is assumed to be the timing of grain filling cessation (n=6, Adj-$r^2 \geq 0.89$ but most of the values were equal or higher than 0.98, $P < 0.0001$).

The inflorescence dry weight at anthesis of wheat and oat was either numerically (2014) or significantly ($P < 0.01$) (2013) heavier with late relative to early SD. The canaryseed cultivars, however, showed contrasting responses between years, but similar within year (Table 6.5). The inflorescence dry weight at anthesis of canaryseed was significantly ($P = 0.01$), positively and linearly associated with main stem inflorescence grain yield at final harvest (Figure 6.7-A).

Tt from TS to anthesis was usually longer for early versus late-seeded plots of all five cultivars, but the differences were more pronounced for canaryseed as shown earlier (Table 6.5). The second component of the inflorescence dry weight at anthesis, the average inflorescence growth rate from TS to anthesis was significantly ($P < 0.01$) higher with late seeding for all five cultivars but only in 2013 while the differences in 2014 were smaller and not significant (Table 6.5). As a result, the average inflorescence growth rate of canaryseed cultivars and not the growth duration, was significantly ($P = 0.005$), positively and linearly associated with its dry weight at anthesis within each SD as well as when considering all year × SD × cultivar combinations (Figure 6.7-C and B).

Canaryseed main stem inflorescence grain filling ceased significantly ($P < 0.01$) later, in terms of Tt, for all five cultivars in 2013, but in 2014 differences were smaller and not significant (Table 6.5).

Table 6.5. Main stem inflorescence dry weight at anthesis (IDW_{An}), elapsed thermal time between terminal spikelet and anthesis (Tt_{TS-An}), average inflorescence growth rate during that phase ($AIGR_{TS-An}$), elapsed thermal time from crop emergence to main stem inflorescence filling cessation (Tt_{IFC}), main stem inflorescece filling duration (Tt_{IFD}), main stem inflorescence dry weight at final harvest (IDW_{FH}) and average main stem inflorescence filling rate (AIFR) for three canaryseed, one spring wheat and one oat cultivar seeded early and late in 2013 and 2014.

Year	Cultivar	Seeding date	Estimates						
			IDW_{An} (g)	Tt_{TS-An} (°Cd)	$AIGR_{TS-An}$ (g °Cd^{-1})	Tt_{IFC} (°Cd)	Tt_{IFD} (°Cd)	IDW_{FH} (g)	AIFR (g100°Cd^{-1})
2013	Togo	Early	0.145	-	-	1249	511	0.472	0.064
		Late	0.277	-	-	1401	588	0.899	0.106
		P-value[1]	***	-	-	**	*	***	*
	Bastia	Early	0.146	485	0.030	1209	476	0.442	0.062
		Late	0.262	352	0.075	1354	541	0.714	0.083
		P-value	***	***	***	**	ns	**	*
	Keet	Early	0.178	461	0.039	1265	488	0.784	0.125
		Late	0.236	340	0.070	1455	520	0.832	0.117
		P-value	*	*	***	**	ns	ns	ns
	Barrie	Early	0.200	499	0.040	1279	531	1.184	0.186
		Late	0.265	448	0.059	1443	704	1.419	0.168
		P-value	**	***	**	*	*	*	ns
	Morrison	Early	0.281	419	0.067	1198	516	1.595	0.255
		Late	0.424	377	0.112	1309	640	2.302	0.307
		P-value	**	**	***	+	+	*	ns
		$SEM^{E, 2}$	0.0109	15.6	0.0024	11.7	12.4	0.0450	0.0101
		P-value	***	*	***	***	*	***	***
		SEM^{L},	0.0121	14.9	0.0043	49.4	45.5	0.0867	0.0277
		P-value	***	***	***	ns	+	***	***
2014	Togo	Early	0.243	522	0.047	1386	550	0.915	0.123
		Late	0.212	439	0.049	1366	488	0.645	0.088
		P-value	ns	**	ns	ns	*	**	*
	Bastia	Early	0.249	556	0.045	1318	475	0.616	0.077
		Late	0.194	503	0.039	1339	509	0.601	0.078
		P-value	+	*	ns	ns	ns	ns	ns
	Keet	Early	0.252	495	0.051	1412	558	1.096	0.152
		Late	0.231	467	0.050	1450	445	0.849	0.126
		P-value	ns	ns	ns	ns	*	*	ns
	Barrie	Early	0.255	492	0.052	1286	461	1.407	0.250
		Late	0.275	468	0.059	1278	497	1.185	0.184
		P-value	ns	*	ns	ns	*	ns	*
	Morrison	Early	0.342	448	0.077	1261	489	1.724	0.281
		Late	0.385	427	0.090	1279	525	1.620	0.236
		P-value	ns	+	ns	ns	ns	ns	ns
		SEM^{E}	0.0192	9.8	0.0044	9.8	11.8	0.1011	0.0174
		P-value	*	***	***	***	***	***	***
		SEM^{L},	0.0237	16.8	0.0045	26.0	31.5	0.0987	0.0181
		P-value	***	*	***	***	ns	***	***

[1]ns, +, *, ** and *** used to denote that the statistical significance of the difference of the means within a year × seeding date and a year × cultivar combination is >0.1, <0.1, <0.05, <0.01, and <0.001.

[2]SEM stands for Standard Error of Mean and superscripts E and L are used to denote the SEM which may be used for cultivar means comparison within early and late seeding date within each year, respectively.

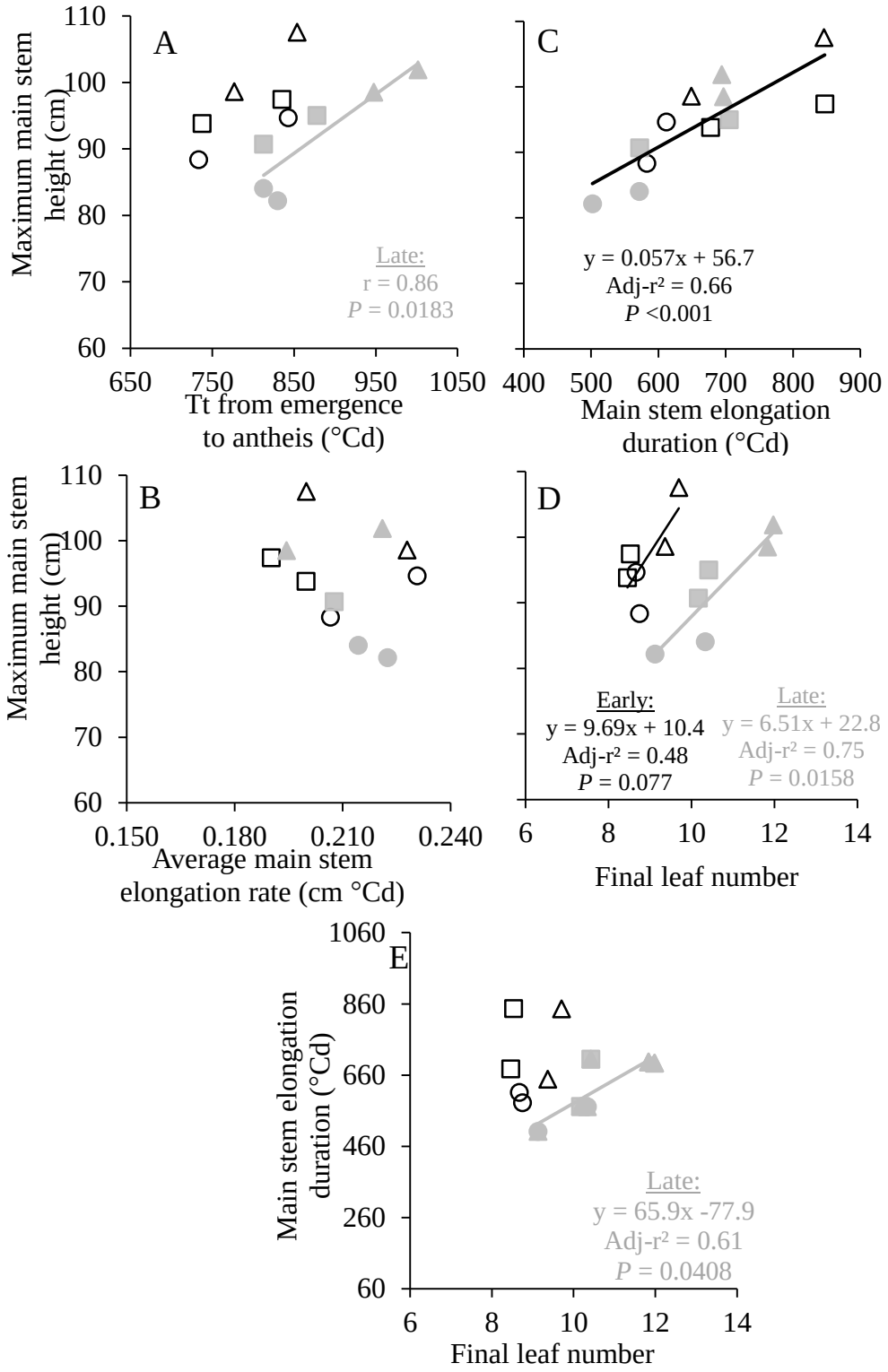

Figure 6.6. Maximum main stem height versus the elapsed thermal time from crop emergence to anthesis (A); the average stem elongation rate (B); the main stem elongation duration (C); the final leaf number (D) and main stem elongation duration versus the final leaf number (E) for the canaryseed cultivars CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) seeded early (open symbols) and late (grey-closed symbols) in 2013 and 2014.

Main stem inflorescence grain yield was more related to the inflorescence dry weight at final harvest than to the inflorescence harvest index, although significant (P = 0.01) association was also found for the late-seeded crops only (Figure 6.8-A and B). As a result, the inflorescence dry weight at harvest responded similarly to that at An.

Differences between SDs in the average inflorescence filling rate and duration were inconsistent across years (Table 6.5), although wheat had a significantly (P < 0.05) longer duration and numerically or significantly (P < 0.01) lower rate with late seeding. In general, the rate, and to a lesser extent the duration (i. e. for early-seeded crops only), were associated with main stem inflorescence grain yield (Figure 6.8-C and D).

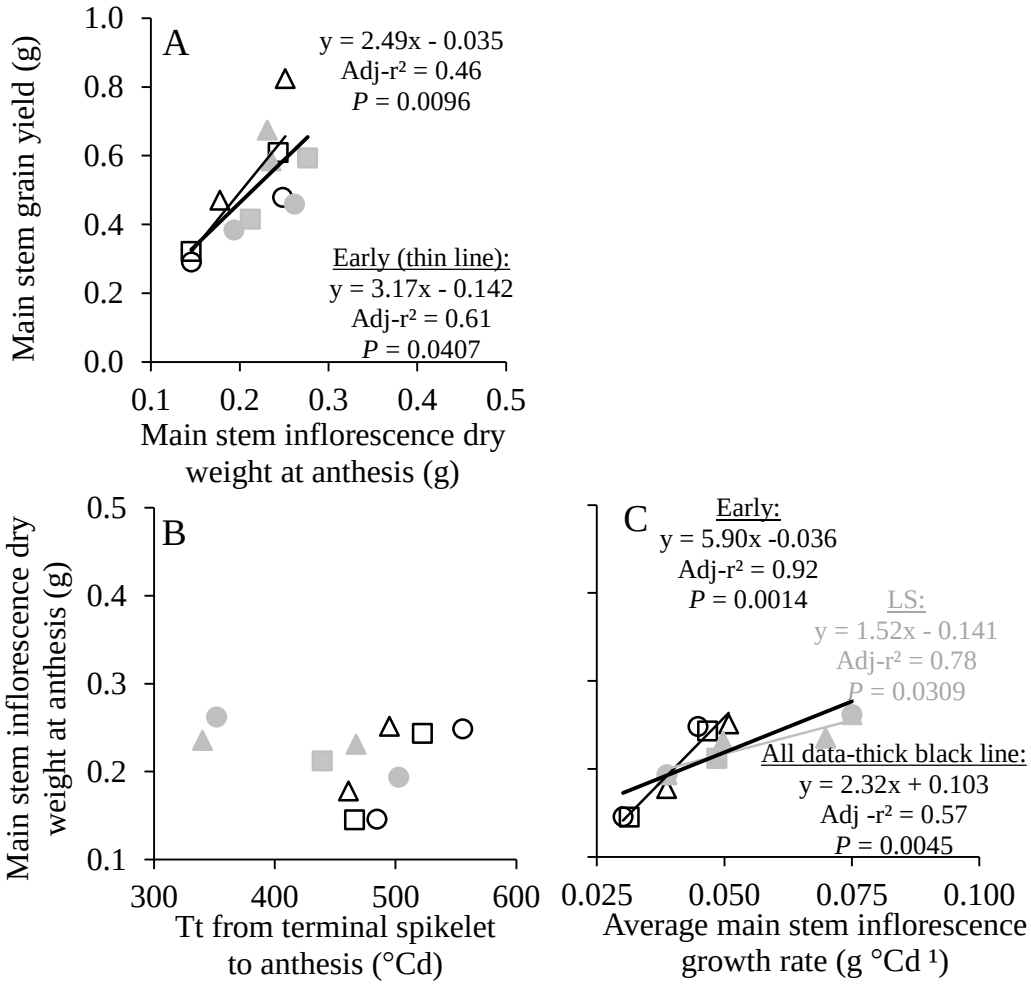

Figure 6.7. Main stem inflorescence grain yield versus the main stem inflorescence dry weight at anthesis (A); main stem inflorescence dry weight at anthesis versus the elapsed thermal time from terminal spikelet to anthesis (B) and versus the average main stem inflorescence growth rate up to anthesis (C) for the canaryseed cultivars CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) seeded early (open symbols) and late (grey-closed symbols) in 2013 and 2014.

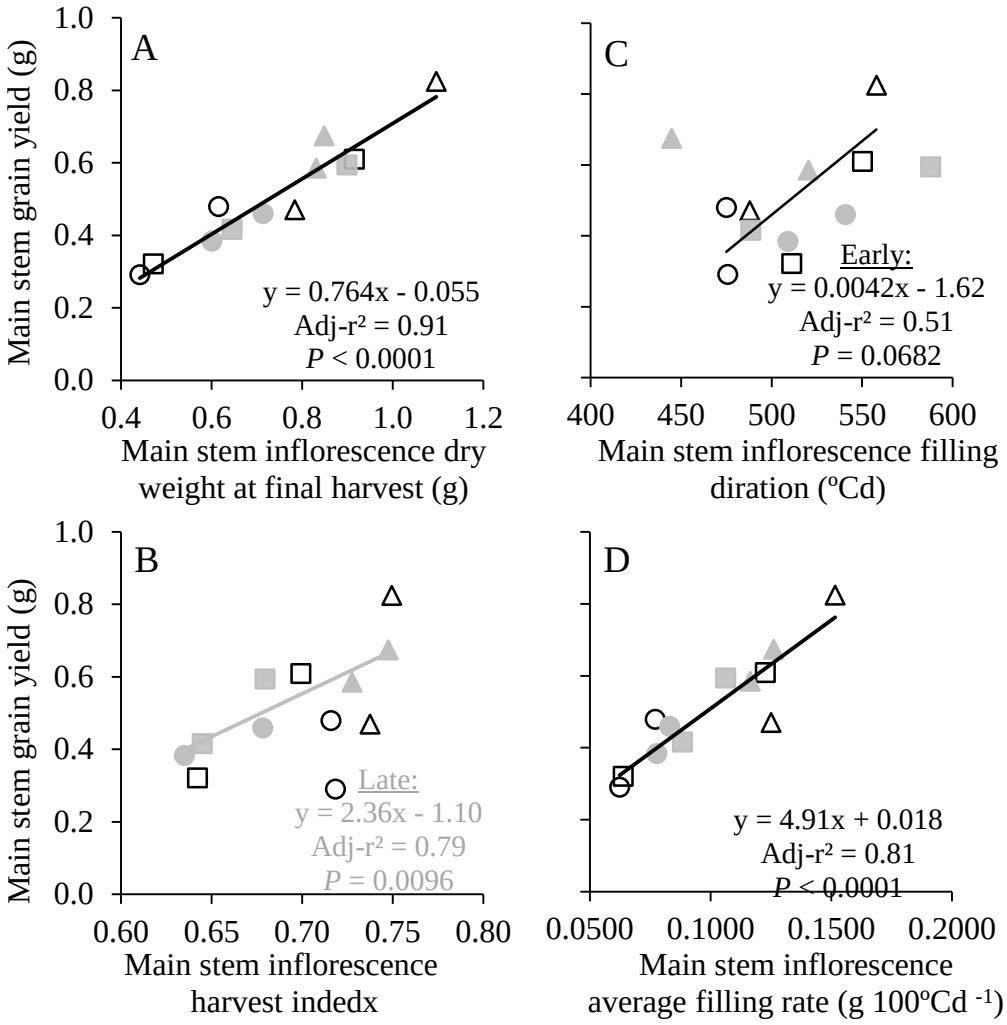

Figure 6.8. Main stem grain yield versus the main stem inflorescence dry weight at final harvest (A); the main stem inflorescence harvest index (B); the main stem inflorescence filling duration (C) and the main stem inflorescence average filling rate (E) for the canaryseed cultivars CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) seeded early (open symbols) and late (grey-closed symbols) in 2013 and 2014.

6.3.2.4 Tiller biomass accumulation

All five cultivars grew tillers irrespective of the date of seeding, which is shown by the cumulative dry weight of tiller shoots at different phenological stages (Figure 6.9 and Appendix 16). In general, canaryseed cultivars allocated more dry matter to growing tillers especially compared to oat and to a lesser extend compared to wheat. Keet allocated the highest tiller biomass at TS than all other cultivars in both years, likely because Keet developed slower than all other cultivars. However, the dry matter allocation pattern to tiller shoots differed between the two years, at least up to anthesis. Although tiller shoot biomass was similar or slightly lower with late seeding for all five cultivars in 2014, in 2013 dry matter allocated to tiller shoots by late-seeded crops was at least double than allocated by early-seeded crops.

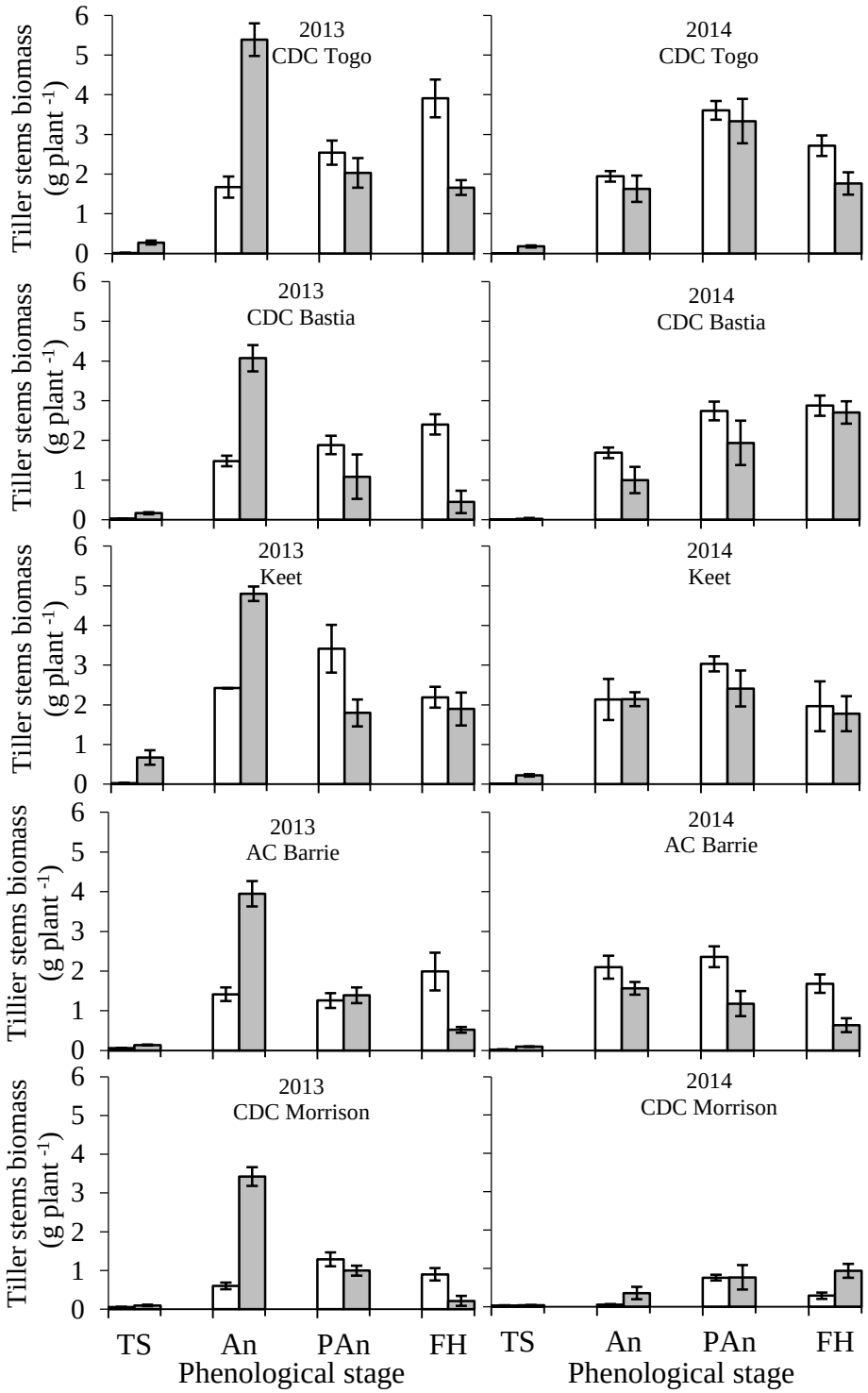

Figure 6.9. Tiller shoot allocated biomass at terminal spikelet (TS), anthesis (An), post-anthesis (PAn) and final harvest (FH) for three canaryseed, one spring wheat and one oat cultivar seeded early (empty bars) and late (grey-closed bars) in 2013 and 2014. Vertical symbols at the top of the bars represent standard error when visible.

Post- anthesis, the difference between the SDs in tiller biomass was relatively small, similar between the years and the five cultivars and mainly not significant. At final harvest, dry matter allocated to tiller shoots in 2014 was either similar between the SDs or less for the late-seeded crops, while in 2013 the differences were more pronounced and often significant ($P < 0.05$).

6.3.3 Main stem- and tiller-derived grain yield

Across all year × SD × cultivar combinations, main stem grain yield of canaryseed plants ranged from 0.23 to 0.83 g/main stem (Appendix 17). For the last two years of the study, canaryseed main stem grain yield ranged from 0.29 to 0.83 g/main stem, while that of wheat and oat ranged from 0.89 to 1.19 g/main stem and from 1.40 to 1.95/main stem, respectively. Differences in canaryseed main stem grain yield due to SDs did occur and cultivars showed similar responses within environments but contrasting responses among environments.

Tiller grain yield of canaryseed cultivars across all year × SD × cultivar combinations ranged from 0.13 to 2.29 g/plant (Appendix 17). For the last two years, it ranged from 0.13 to 1.18 g plant^{-1} with a wider range compared to wheat (0.24 to 1.0 g plant^{-1}) and oat (0.11 to 0.84 g plant^{-1}). The SD effect on tiller-derived grain yield of canaryseed, unlike that of the main stem grain yield, was significant ($P < 0.01$) mainly for CDC Togo and generally for half of the year × cultivar combinations. However, the trend across SDs was not consistent among the years. Keet did not show significant changes in tiller-derived grain yield across SDs in both years, even though late seeding means were lower than the early seeding means by up to 42% (eg, in 2013).

Main stem grain yield of wheat and oat was higher than that of canaryseed and with narrower ranges. Canaryseed tillers, however, produced comparable yields to wheat and higher yields than oat. Tillers of canaryseed contributed by 22 to 85% of the total plant grain yield across all year × SD × cultivar combinations. For the last two years, the contribution of tillers to whole plant grain yield ranged from 22 to 79% and the corresponding ranges for wheat and oat were 20 to 45% and 5 to 28%, respectively. In general, the canaryseed cultivars had a similar trend in tiller-derived grain yield changes between within-year SDs, which however differed from year to year.

SD did affect the harvest index of the main stem, but cultivars responded differentially between the SDs across the years (Table 6.7). The tiller harvest index of canaryseed was numerically lower with late seeding but differences were moderate (no higher than 13% and often not significant). SD moderately affected the main stem inflorescence harvest index, but affected it inconsistently across the years and mainly not significantly. In contrast, canaryseed tiller inflorescence harvest index was often significantly ($P < 0.05$) or nearly significantly ($P <$

0.1) reduced by delayed seeding. However, differences were not consistent across the years. The harvest index of tiller inflorescence of wheat was numerically or significantly ($P < 0.05$) reduced with late seeding and for oat the response was inconsistent and not significant.

Considering all year × SD × cultivar combinations, canaryseed cultivars grew at least three, and in many cases even more, primary tillers of agronomic importance, which is defined here as a tiller that produced a substantial grain yield (at least 10% of that produced by the main stem inflorescence) (Figure 6.12). Some treatments formed even higher-ranked (above the third) primary tillers and even secondary ones that were yield-wise important. Often, especially with early seeding, CDC Bastia and CDC Togo produced tillers that yielded similarly to or even more than the main stem. Keet formed tillers that produced considerably lower grain yield compared to the main stem in all environments, except in 2012. For the last two years, both wheat and oat formed fewer tillers of agronomic importance, compared to those formed by the canaryseed cultivars especially with early SDs (Figure 6.13). In addition, the wheat or oat tillers in all SDs in both years produced grain yields that were considerably lower than those produced by the main stem inflorescences. Wheat in 2012, however, did form tillers that contributed to grain yield like the tillers formed by the canaryseed cultivars. In 2012, the main stem yield of oats and that from individual tillers was not recorded due to yield loss from shattered seeds.

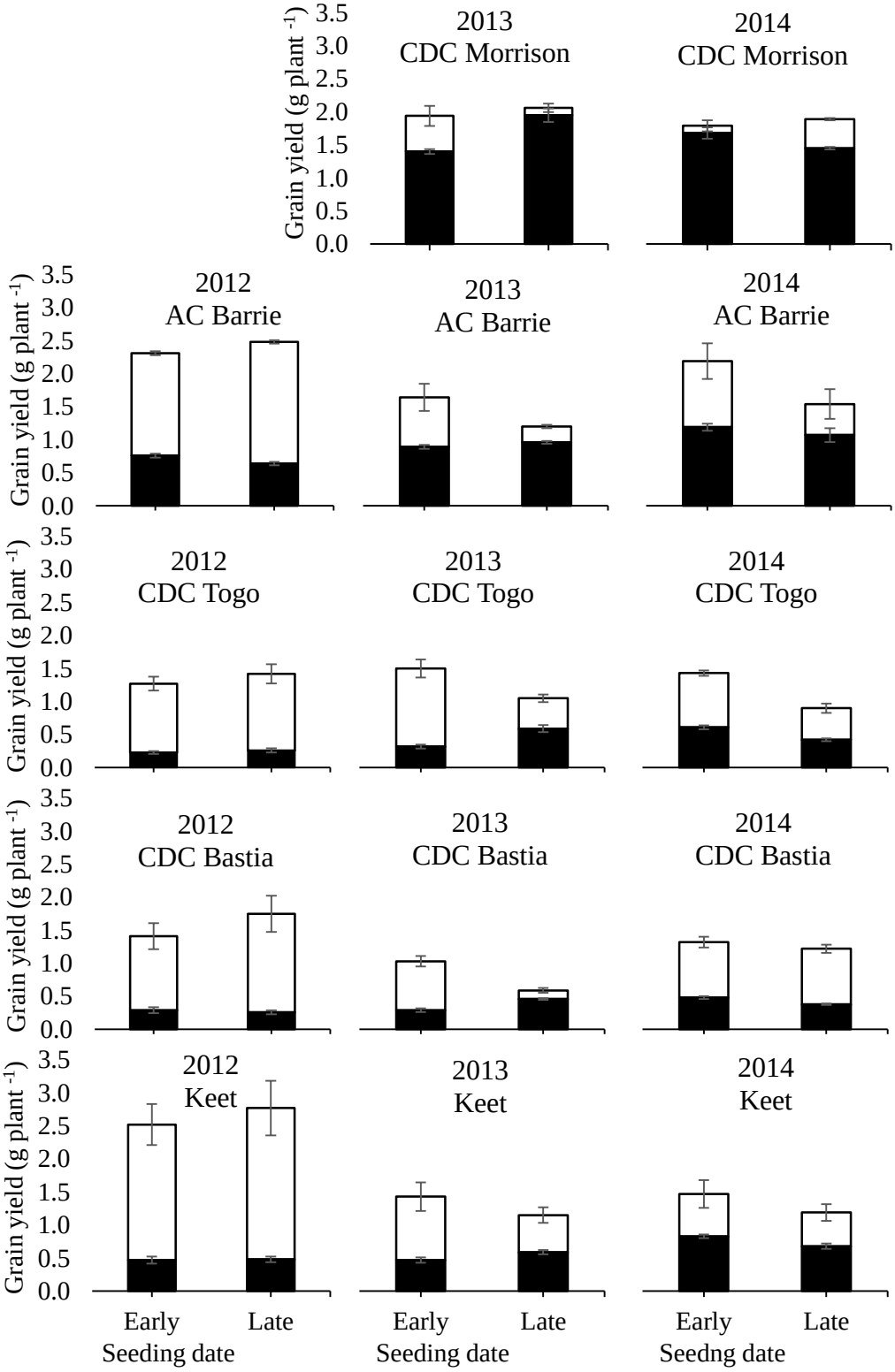

Figure 6.10. Main stem- (solid bars) and tiller-derived (non-filled bars) grain yield (g plant $^{-1}$) for three canaryseed, one spring wheat and one oat cultivar seeded early and late in 2012, 2013 and 2014. Symbols at the top of the bars represent standard error. Means separation may be found in the appendices in Appendix 17.

Table 6.6. Main stem, tiller stems and their inflorescence harvest indices for three canaryseed, one spring wheat and one oat cultivar seeded early and late in 2012, 2013 and 2014.

Cultivar	Stat. An.[1]	2012		Sign.[4]	2013		Sign.	2014		Sign.
		Early	Late		Early	Late		Early	Late	
					Main stem harvest index					
Togo		-	-	-	0.21(0.014)^{d}	0.26(0.013)^{c}	*[5]	0.28(0.014)^{b}	0.23(0.008)^{b}	*
Bastia		-	-	-	0.23(0.011)^{cd}	0.23(0.014)^{c}	ns	0.27(0.005)^{b}	0.26(0.009)^{b}	ns
Keet		-	-	-	0.27(0.012)^{c}	0.24(0.014)^{c}	ns	0.29(0.003)^{b}	0.28(0.006)^{b}	*
Barrie		-	-	-	0.41(0.007)^{b}	0.36(0.014)^{b}	*	0.41(0.015)^{a}	0.48(0.050)^{a}	ns
Morrison		-	-	-	0.47(0.004)^{a}	0.48(0.009)^{a}	ns	0.46(0.004)^{a}	0.50(0.004)^{a}	**
	SEM[2]	-	-	-	0.012	0.017		0.011	0.021	
	Sign.[3]	-	-	-	***	***		***	***	
					Tiller shoots harvest index					
Togo		-	-	-	0.27(0.010)^{b}	0.24(0.014)^{c}	ns	0.31(0.017)^{a}	0.27(0.007)^{c}	+
Bastia		-	-	-	0.27(0.008)^{b}	0.25(0.014)^{c}	ns	0.29(0.003)^{a}	0.31(0.010)^{bc}	ns
Keet		-	-	-	0.30(0.004)^{b}	0.27(0.013)^{c}	*	0.32(0.007)^{a}	0.29(0.012)^{bc}	*
Barrie		-	-	-	0.41(0.006)^{a}	0.39(0.013)^{b}	ns	0.40(0.016)^{a}	0.33(0.025)^{b}	+
Morrison		-	-	-	0.44(0.021)^{a}	0.48(0.005)^{a}	ns	0.29(0.145)^{a}	0.47(0.009)^{a}	ns
	SEM	-	-	-	0.014	0.020		0.063	0.014	
	Sign.	-	-	-	***	***		ns	***	
					Main stem inflorescence harvest index					
Togo		0.53(0.034)^{b}	0.50(0.033)^{b}	ns	0.64(0.028)^{b}	0.68(0.012)^{b}	ns	0.70(0.026)^{c}	0.65(0.010)^{b}	+
Bastia		0.59(0.031)^{b}	0.54(0.023)^{b}	ns	0.72(0.035)^{b}	0.68(0.016)^{b}	ns	0.73(0.006)^{bc}	0.62(0.061)^{b}	ns
Keet		0.72(0.015)^{a}	0.69(0.017)^{a}	ns	0.74(0.017)^{b}	0.72(0.009)^{b}	ns	0.75(0.007)^{bc}	0.75(0.008)^{ab}	ns
Barrie		0.76(0.005)^{a}	0.71(0.013)^{a}	**	0.75(0.014)^{b}	0.71(0.028)^{b}	ns	0.78(0.004)^{b}	0.85(0.100)^{a}	ns
Morrison		-	-	-	0.90(0.003)^{a}	0.87(0.023)^{a}	ns	0.90(0.005)^{a}	0.89(0.006)^{a}	ns
	SEM	0.024	0.031		0.026	0.023		0.016	0.054	
	Sign.	***	***		***	***		***	**	
					Tiller shoots inflorescences harvest index					
Togo		0.58(0.029)^{b}	0.56(0.025)^{b}	ns	0.70(0.006)^{c}	0.64(0.018)^{c}	*	0.79(0.070)^{a}	0.66(0.009)^{c}	ns
Bastia		0.67(0.009)^{a}	0.59(0.020)^{b}	**	0.72(0.006)^{bc}	0.66(0.010)^{bc}	**	0.74(0.012)^{a}	0.70(0.010)^{bc}	+
Keet		0.72(0.013)^{a}	0.68(0.019)^{a}	+	0.75(0.010)^{bc}	0.70(0.022)^{bc}	+	0.75(0.012)^{a}	0.74(0.022)^{b}	ns
Barrie		0.65(0.024)^{ab}	0.62(0.030)^{ab}	ns	0.79(0.035)^{b}	0.73(0.014)^{b}	ns	0.78(0.005)^{a}	0.65(0.028)^{c}	*
Morrison		-	-	-	0.88(0.015)^{a}	0.89(0.008)^{a}	ns	0.60(0.015)^{a}	0.89(0.015)^{a}	ns
	SEM	0.020	0.003		0.017	0.021		0.132	0.019	
	Sign.	***	0.035		***	***		ns	***	

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Significance of the statistical test between seeding date means within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [5]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. Standard error in brackets.

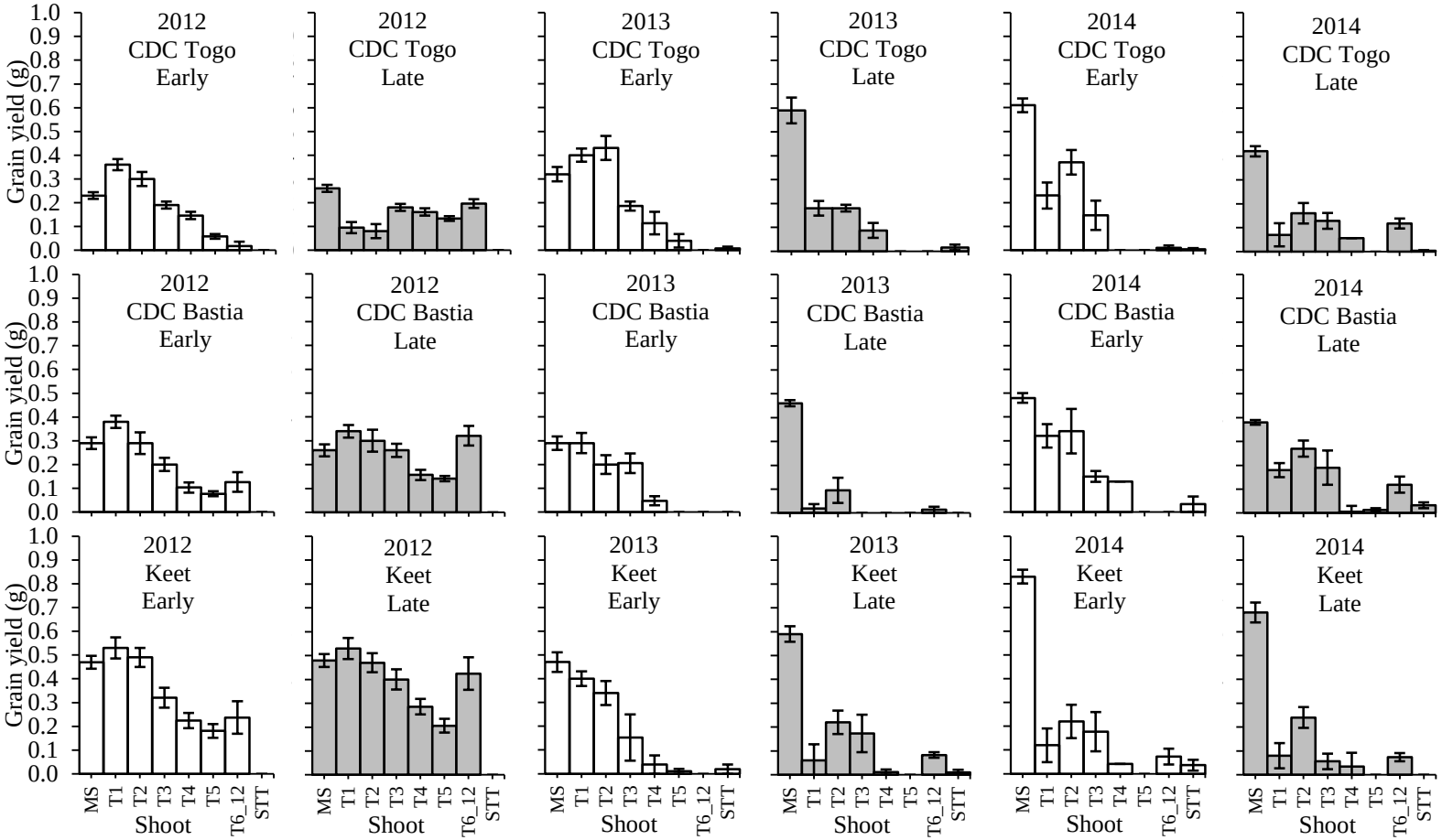

Figure 6.11. Main stem- (MS) and tiller- (T) derived grain yield for three canaryseed cultivars seeded early (empty bars) and late (grey-closed bars) in 2012, 2013 and 2014. The number accompanying the letter T denotes the leaf on MS from the sheath of which the tiller grew. The abbreviation T_{6_12} is used for the sum of the grain yield derived from T6 to T12. STT abbreviation is used for the sum of the grain yield derived from the secondary, tertiary and higher-ranked tillers.

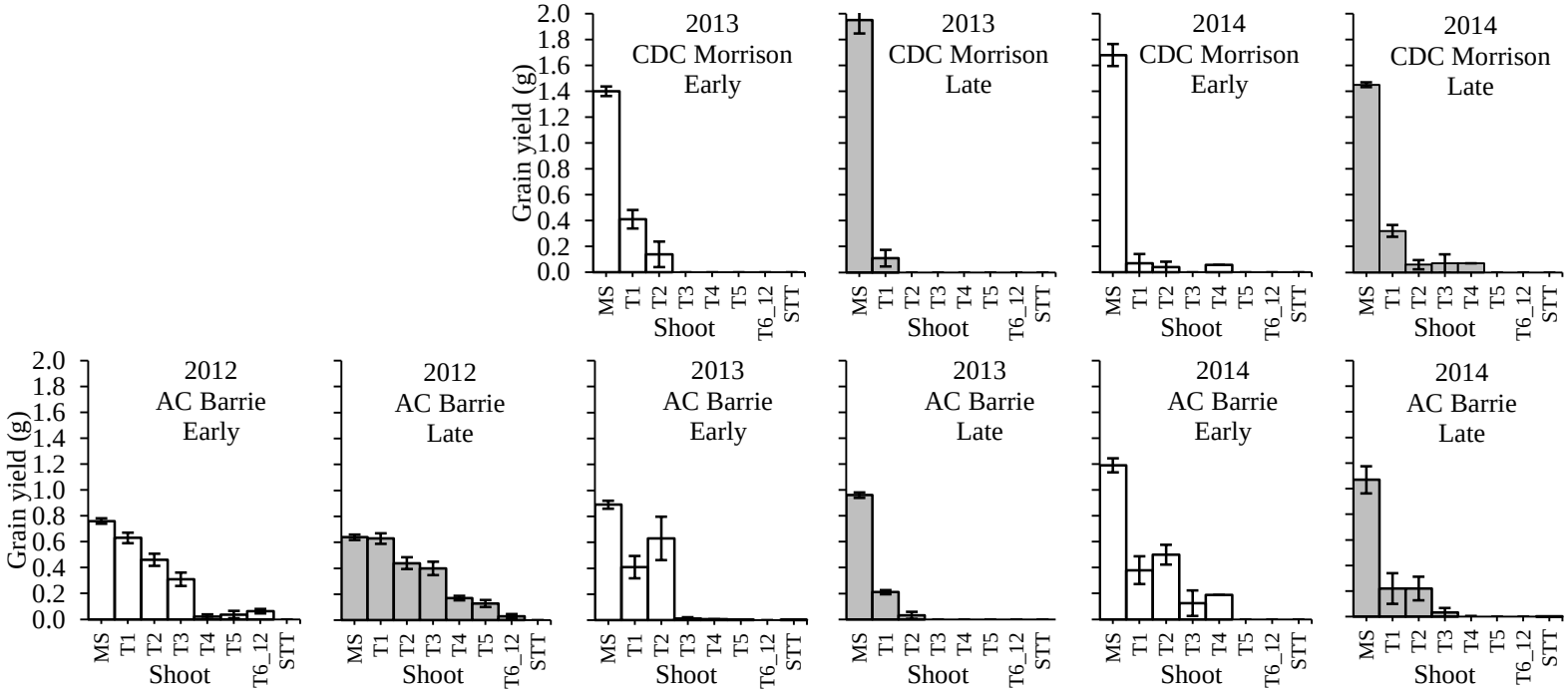

Figure 6.12. Main stem- (MS) and tiller- (T) derived grain yield for one spring wheat and one oat cultivar seeded early (empty bars) and late (grey closed bars) in 2012, 2013 and 2014. The number accompanying the letter T denotes the leaf on MS from the sheath of which the tiller grew. The abbreviation T_{6_12} is used for the sum of the grain yield derived from T6 to T12. STT abbreviation is used for the sum of the grain yield derived from the secondary, tertiary and higher-ranked tillers.

6.4 Discussion

6.4.1 Plant phenology and morphology

Time from seeding to crop emergence is determined mainly by temperature for wheat (eg, Brown et al., 2013 and references therein) and oat (Sonego et al., 1997), assuming adequate soil bed moisture for seed imbibition. That seems to hold for canaryseed cultivars as well. The one extra day difference in crop emergence time between canaryseed cultivars and the other two crop species recorded with the very late SD in 2014 might be associated with lower seedling vigor possibly affected by lower seedbed moisture due to soil crusting. The latter has been shown to be a main seedbed variable determining seed vigour (Finch-Savage and Bassel, 2015 and references therein).

The variability of canaryseed cultivars among environments in Tt to anthesis was associated with SD. Delayed seeding postponed the attainment of certain pre-anthesis phenological stages, such as that of TS formation and FLL appearance, and eventually delayed anthesis itself. In contrast, the estimated duration of pre-anthesis phenological phases of the wheat and oat were either consistent (2014) or increased with delayed seeding (2013), but to a much smaller extent compared to canaryseed. The longer phenological pre-anthesis phases of canaryseed were mainly explained by the increased FLN, as observed for other temperate cereals (see later for references) and not by the changes in the average phyllochron. However, even with the early SDs in 2013 and 2014, canaryseed reached TS earlier or at the same Tt as wheat and oat, while canaryseed plants still formed similar or higher FLN than the other two species. The response of FLN to delayed seeding could be explained by the higher leaf initiation rate of canaryseed cultivars relative to the other two species, as discussed in Chapters 3 and 4. A similar FLN response of barley was reported by Miralles et al. (2001) due to the faster leaf initiation rate of barley cultivars compared to wheat cultivars. The relatively small differences for the estimated duration of pre-anthesis phases of wheat and oat were due to small differences in FLN across environments. As a result, Tt to anthesis of wheat and oat changed slightly across environments. Delayed phenological development due to increased FLN has also been reported for wheat (Hay and Kirby, 1991), barley (Miralles et al., 2001), oat (Sonego et al., 2000), and triticale (Giunta et al., 2001; Estrada-Campuzano et al., 2008). According to the literature, differences in FLN in wheat mainly resulted from the response of plants to low-temperature vernalization and/or photoperiod (Brooking et al., 1995; Mahfoozi et al., 2001a and b; Brooking and Jamieson, 2002; Allard et al., 2012; Steinfort et al., 2017), with photoperiod affecting the phenological

development during or after the vernalization process (Brooking and Jamieson, 2002; Brown et al., 2013).

Canaryseed is assumed to be a long day plant as explained in Chapters 4 and 5. When long day plants from lower latitudes are exposed to long day conditions of higher latitudes, anthesis is likely to be hastened assuming that no other abiotic factors limit development. Based on the results of this study, anthesis of canaryseed cultivars grown under very long photoperiods was delayed, in terms of Tt, with later SDs. The natural photoperiod experienced by young plants of late and very late SDs declined, which could be an argument for the delayed anthesis, with respect to that of early SD. However, assuming any photoperiodic effect to be limited up to anthesis as explained in wheat (Brown et al., 2013), for a period of 55 to 65 days after seeding (850 to 1200 °Cd), the day length for the early and late SDs is at least 16h. That is even longer than the natural prevailing day length in the centre of origin of canaryseed (between 30 and 45^0N) and similar to the upper limit of the range of day lengths shown to have anthesis increasing effect on wheat. Therefore, it is unlikely that the delayed anthesis, at least for the late-seeded plots, was the absolute response of plants to day length up to anthesis. Even the delayed anthesis of the very late-seeded plots can only partially be explained by the declining day length, as the natural day length up to anthesis was at least 14 hours. Apart from that, the duration of the stem elongation phase (TS – anthesis) was negatively associated with the duration from emergence to TS. That means that later SDs showed a shortened duration of the stem elongation phase compared to early SDs and that the potential delay due to photoperiodic effects on the Tt to anthesis of very late SDs was small. All this information may suggest that the delayed anthesis of later seeded canaryseed plants is not likely to be the result of the single photoperiodic effect on plants. The photoperiod, however, might have affected the phenology of canaryseed plants synergistically with temperature on their putative low-temperature vernalization requirement (see Chapter 4). As mentioned earlier, the response of a low-temperature vernalization requirement of a vernalization-sensitive wheat genotype is confined to phenological phases prior to the FI at the stem apex (Brown et al., 2013 and references therein). The photoperiod, however, may affect wheat phenology on both phases, prior to and after the FI. Before the FLN has been determined, phenological response to photoperiod can be differential depending on the temperature and a potential vernalization requirement (Brooking and Jamieson, 2002). In fact, both Brooking and Jamieson (2002) and Mahfoozi et al. (2001a) showed that, in wheat genotypes with a vernalization requirement, the latter may be met faster under shorter photoperiods. In addition, when the vernalization process occurs under higher temperatures (above 8°C), the photoperiod may interact with temperature and long photoperiod

may delay the process (Brooking and Jamieson, 2002; Allard et al., 2012; Brown et al., 2013). Similarly, in the case of later SDs, the elevated temperatures that the plants experienced, especially from the late morning until early evening hours, might have interacted with very long photoperiods to delay the fulfillment of canaryseed vernalization requirement. Such interactive effects between the vernalizing temperature and photoperiod are again expressed through changes in FLN, as they have been also shown in this study.

Regarding the possibility of a faster canaryseed vernalization requirement fulfillment under short(er) day-lengths, in Chapter 4, the results suggested that a short photoperiod, at least that of 8 hours during the vernalizing treatments of canaryseed seedlings was less or as effective in reducing the FLN and the $MHLS_{FI}$, compared to the very long photoperiod of 20h. Thus, a short(er) photoperiod during the vernalization process is unlikely to enable the putative low-temperature vernalization requirement of canaryseed to be met faster than a long photoperiod (eg, 17h or 20h).

On the other hand, the effectiveness of dark conditions in the fulfillment of the canaryseed putative low-temperature vernalization requirement is a possibility that cannot be discarded. In their study of brachypodium (*Brachypodium distachyon*), a member of the same family as canaryseed, Ream et al. (2014) reported that the days to flowering and thus FLN (a strong correlation is reported between the two variables) were reduced under the longer photoperiod in post-vernalizing conditions. That occurred when imbibed seeds were vernalized under an 8-hour photoperiod for several different periods of time during which the imbibed or germinated seeds either did not sense or only later during the vernalizing treatment were able to sense the photoperiod and then exposed to either a 16h or 20h photoperiod for plants outgrowth. In the present study, canaryseed crop emergence occurred on the 9^{th}, 7^{th} and 5^{th} day after seeding in 2013 and on the 12^{th}, 8^{th} and 6^{th} day after seeding in 2014 for the early, late, and very late SDs, respectively. The fewer days between seeding and crop emergence observed with later SDs in both years might be related to a partially met or unmet vernalization requirement that was later phenotypically expressed via an increased FLN on the main stem of plants.

The glabrous canaryseed cultivars CDC Togo and CDC Bastia differed from the pubescent cultivar Keet in their morphology and phenology. For instance, the differences in FLN and the duration from emergence to TS between the early and the later SDs were gradual for both glabrous cultivars. In contrast, Keet showed anthesis abrupt change in both variables from early to later SDs and less variability between the two later SDs. Such differences show that glabrous cultivars are less prone to moderate increments in temperature under very long photoperiods.

Thus, their adaptability to certain environments might be relevant for breeding new glabrous cultivars.

Despite the smaller flag leaf area with late, compared to early, SD in most of year × canaryseed cultivar combinations and the higher canaryseed mean flag leaf area of early versus late-seeded crops, there was no significant correlation between those two response variables. However, Steinfort et al. (2017) recently reported a negative linear relationship between the flag leaf area of wheat isogenic lines with differences in the vernalization requirement and their FLN. Possible explanations for the lack of significance of such a relationship in the present study are that cultivars, not near isogenic lines were used, and that the shallow root system of the canaryseed cultivars might have made the flag leaf area more responsive to abrupt changes in the soil moisture during the period of its growth and expansion. Nevertheless, the flag leaf area of early-seeded canaryseed crops was positively, linearly associated with the main stem inflorescence grain yield. Similarly, Simpson (1968) reported anthesis association between the grain yield per plant and the photosynthetic area above the flag leaf node in wheat and Dimmock and Gooding (2002) reported that gains in green flag leaf area duration were associated with increased grain yield. Interestingly, no relationship between flag leaf area and grain yield was found for the late-seeded canaryseed crops, likely due to the association between grain yield and inflorescence harvest index.

The length of the relatively long main stems of late-seeded canaryseed crops was related to their late inflorescence anthesis (and FLN as these two were shown to be associated) and to the longer,compared to wheat and oat, main stem elongation beyond anthesis. Although long main stems in small grain temperate cereals are generally considered competitors for assimilates with the inflorescence, no significant relationship was found between the stem height and the main stem inflorescence dry weight at anthesis.

6.4.2 Main stem inflorescence growth and grain filling characteristics

The moderately negative correlation found between the duration from emergence to TS with the duration from TS to anthesis is the first to be reported for temperate cereals and it is not in agreement with what has been reported for wheat. Gonzalez-Navarro et al. (2016) reported a slight positive relationship between the two phases for a series of elite wheat cultivars and Estrada-Campuzano et al. (2008) reported lack of association between the two phases for a series of triticale cultivars. A shorter duration of that period would translate into lower photo-assimilate production during that period (assuming unchanged leaf area and incoming solar radiation). Given that in this period, the inflorescence accumulates most of its dry matter,

relatively lower amounts of assimilates are expected to be available for the inflorescence growth with late-seeded canaryseed crops. In addition, the flag leaf area or that of the penultimate leaf (ie, in seven out of nine year × cultivar combinations) was lower with late-seeded, compared to early-seeded, crops. Considering that the main stem height and the main stem inflorescence dry weight at anthesis were not related and that the latter was mainly determined by its average growth rate, it seems to have been more limited by source than by the competition with the main stem. That is in line with the fact that changes in growth rate had a larger impact on the inflorescence dry weight at anthesis of early-seeded than late-seeded crops. The putative source limitation of canaryseed main stem inflorescence dry weight at anthesis agrees with what is widely known in wheat, namely that the main stem inflorescence dry weight at anthesis relates to the assimilate availability during its growth regardless of the causal factor for differences in the availability (ie, Fischer and Stockman, 1980; Fischer, 1985; Siddique et al., 1989; Fischer, 1993; Miralles et al., 2000). The positive linear association of the main stem inflorescence dry weight at anthesis and the inflorescence grain yield found for the canaryseed cultivars is also broadly known in wheat, given that grain yield in small grain temperate cereals is usually determined by the grain number.

The main stem grain yield was also associated with its inflorescence dry weight at final harvest, although for the late-seeded crops the latter was also associated with the inflorescence harvest index. That relationship found with late-seeded crops could be either due to aborted florets/floret primordia or due to lack of resources available to sustain a grain filling rate at the required level to fill the active grain-sinks. Regarding the floret/floret primordia abortion, it has been shown to be determined by the assimilate availability right before anthesis in wheat (Fischer, 1985; Miralles et al., 2000; González et al., 2005a and b;), barley (Arisnabarreta and Miralles, 2008) and triticale (Estrada-Campuzano et al., 2012). Thus, the idea that the main stem inflorescence dry weight at anthesis seems to have been mainly source limited is further supported while the same seems likely for the grain filling duration given that main stem-derived grain yield was positively linearly associated with its average grain filling rate and not by the grain filling duration.

In 2014, tiller biomass accumulation at final harvest of the late-seeded wheat and the canaryseed cultivars CDC Togo and Keet was reduced compared to post-anthesis. Similarly in 2013, but to a much greater extent, and for all five cultivars, tiller biomass of late-seeded crops at final harvest was lower, compared to that at anthesis. This reduction could be explained by carbon mobilization from tillers to main stems. In 2013 early-seeded crops received 140 mm of rainfall in a two-week period up to around five days prior to anthesis and received another 50

mm near and right after anthesis. The late-seeded crops received the same amount of rainfall, but it coincided with different phenological stages, as the high rainfall period ended around two weeks prior to anthesis and from that time to anthesis a sum of 50 mm was well spread throughout that period. In addition, late-seeded crops in 2013 received no rainfall for about 10 days after anthesis. In contrast in 2014, early-seeded crops received 100 mm of rainfall right after anthesis and late-seeded ones received 60 mm right prior to anthesis, raising the total amount of rainfall up to anthesis to 190 mm. That was about 25 mm more than the late-seeded crops received in 2013. The higher water deficit experienced by the late-seeded crops compared to the early-seeded ones in 2013 would support a potential mobilization of carbon reserves from tillers to the main stem so the main stem could cover its inflorescence grain filling requirements. Similarly, Palta et al. (1994) reported that water deficit during grain filling resulted in the translocation of water-soluble carbohydrates from tillers to the main stem spike in wheat.

6.4.3 Main stem- and tiller-derived grain yield

Canaryseed cultivars had a low main stem grain yield (approximatelly half of the corresponding yield of wheat and a third of that of oat when averaged over environments) and high main stem grain yield variability (approximatelly a three-fold higher variability than for wheat and oat across environments). Strategies to increase photo-assimilate supply to the inflorescence might be relevant to increase main stem grain yield and to reduce its variability. Such a strategy could be related to partitioning the phenological phases, focusing on the period between emergence and TS. Keeping the duration from emergence to TS similar to that of wheat and oat with early SDs (like CDC Bastia and CDC Togo with early SDs) and without substantially changing the anthesis time would likely provide more time to the phase from TS to anthesis and allow more photo-assimilates to be allocated to the inflorescence by anthesis. In addition, a stable FLN (by keeping the emergence to TS period short) would likely lower somewhat the main stem leaf area but would indirectly increase the leaf area of the upper phytomers due to the higher FLN of canaryseed plants resulting in lower leaf areas of the upper phytomers. Also, the increased FLN of the pubescent cultivar compared to the glabrous ones in many environments, including two out of three early SDs (the difference in 2012 might have been missed due to the lack of leaf marking), might be related to genotypic variability relevant to crop's low low and/or unstable grain yield. The increased FLN on the main stem of Keet could be used as a strategy to increase the main stem leaf area and potentially increase the main stem grain yield. However, such a strategy would have as a prerequisite the shortening of the emergence to TS phase for the reason discussed above.

The high tiller-derived grain yield, relative to that of the main stem of canaryseed found for all early-seeded crops and less often with late-seeded ones, was the result of the high number of tillers produced and/or the contribution of lower-ranked tillers to whole plant grain yield. Two studies conducted previously in Saskatchewan, Miller (2000) and May et al. (2012a) indirectly addressed the importance of tiller-derived grain yield. However, in the present study, the importance of tiller-derived grain yield is quantitatively supported by the sum of all tiller-derived grain yield per plant, by the individual tiller-derived grain yield and by the positively linear association of a plant's grain yield with the tiller-derived grain yield (Appendix 18). Although such a relationship was found for wheat as well, the slope of the relationship for canaryseed plants was 15% higher compared to that of wheat, meaning that the contribution of tiller-derived grain yield in canaryseed has a greater impact on total plant grain yield than in wheat. The reported importance of tiller-derived grain yield in canaryseed contrasts with that of other cereals. Grain yield production by tillers is reported to be modest for cereals such as oat, durum wheat and triticale when grown under the long days of high latitudes, with the exception of two-row barley (Peltonen-Sainio et al., 2009). In temperate environments of lower latitudes, wheat tillers and main stems contribute more equally to plant grain yield, while in triticale most of the grain yield is main stem-derived (Sweeney et al., 1992; Lopez-Castaneda and Richards, 1994). In environments such as those encountered in 2012, the importance of tiller-derived grain yield in canaryseed was even more pronounced. In general, in environments where tiller-derived grain yield was substantially reduced, this coincided with whole canaryseed plant grain yield reduction, although main stem grain yield was relatively more stable.

The appearance and survival of higher-order tillers in canaryseed, especially with early-seeded crops, as shown by the tiller-derived grain yield production (Figure 6.12), might relate to potentially high amounts of radiation reaching deeper leaf canopy layers, generating a surplus of photo-assimilates with close vascular proximity to the tiller buds of higher-order leaves on the main stem. The number of growing tillers has been explained by a higher accumulation of intercepted radiation during the jointing-heading phase in barley (Abeledo et al., 2004). However, tiller survival and their subsequent contribution to whole plant grain yield was lower with late-seeded canaryseed crops. Dreccer et al. (2013) discussed the possibility of relatively higher mortality of higher-ranked tillers in relation to different plant densities as a result of lower C-sink priority. Different plant densities generate differences in photo-assimilate availability similar to those discussed earlier regarding the assimilate supply of the main stem inflorescence prior and beyond anthesis, especially with late-seeded canaryseed crops. It is

possible therefore that lower C-source for grain filling of main the stem inflorescence is related to the senescence of lower C-sink, higher-ranked, tillers more prominently observed with late seeding. On the other hand, a potential relation of the relatively higher water deficit that the plants encountered with late seeding, especially in 2013, with the senescence of higher-ranked tillers and the subsequent C-mobilization should not be disregarded.

6.5 Conclusions

Delayed seeding of canaryseed cultivars on the Canadian Prairies delayed the timing of certain phenological stages such as that of FI, TS and anthesis. The length of the pre-anthesis phases of late-seeded crops were altered differentially and differences between types of cultivars were found. Such changes were accompanied by morphological changes such as the FLN, the main stem height and the top phytomer leaf area. In contrast, wheat and oat showed generally no, or relatively smaller differences, with regards to these response variables between the SDs. A putative canaryseed vernalization requirement is consistent with the observations made in these experiments. Consequently, the canaryseed main stem inflorescence dry weight up to anthesis as well as the grain filling period were likely C-source limited, especially with late SDs and to a greater extent compared to wheat and oat. With regards to grain yield, environments where canaryseed tiller-derived grain yield was substantially reduced coincided with whole plant grain yield reduction, although main stem grain yield was relatively more stable. However, grain yield of wheat and oat usually depended more on main stem yield.

Transition section between Chapter 6 and Chapter 7

Unmet vernalization requirements of vernalization sensitive temperate cereal genotypes affects their phenological development via changes in the length of individual pheno-phases and/or entire life cycle. Such changes often occur with simultaneous morphological changes such as stem height, individual leaf, plant or crop leaf area and tiller number. Eventually their grain yield is often negatively affected. Indeed, in the previous chapter (Chapter 6) it was shown that delayed seeding of canaryseed cultivars on the Canadian Prairies delayed the timing of FI, TS and anthesis. The length of the pre-anthesis phases of late-seeded canaryseed, spring wheat and oat were altered differentially with canaryseed showing greater response relative to wheat and oat as well as differences between cultivars. Such changes were accompanied by morphological changes closely related to grain yield. Consequently, canaryseed plant grain yield reduction with delayed seeding was greater relative to that of wheat and oat. This was true especially when canaryseed tiller-derived grain yield was substantially reduced while main stem grain yield was relatively more stable, though likely C-source limited. In contrast, grain yield of wheat and oat plants usually depended more on main stem yield.

Unmet vernalization requirements of vernalization sensitive temperate cereal genotypes affect their crop biomass production. This is because crop phenological development and/or growth mismatches the seasonal weather conditions especially in short season rainfed growing environemnts such as those often met in the Canadian Prairies. Consequently, differences in the ammounts of captured resources and/or utilization occur with concomitant impact on the distribution of crop biomass to the harvestable product that is the grain yield and its components. Therefore, the objectives of the following chapter (Chapter 7) are i) to determine if the reduced grain yield of canaryseed is associated with crop biomass differences and biomass components or to the dry matter allocation to the grain, ii) to compare the response of canaryseed to environmental conditions with that of spring wheat and oat that have no, or minimal, vernalization requirements and iii) to investigate genotypic variability for crop biomass production and its distribution to the harvestable product among canaryseed cultivars.

Chapter 7 Differences between annual canarygrass, spring wheat and oat as related to seeding date in a semi-arid environment: Biomass, yield and their components

7.1 Introduction

Annual canarygrass (*Phalaris canariensis*) suffers from unstable grain yield when grown under the long days and variable weather conditions typical of the Canadian prairies. Previous studies on seeding date (SD) addressed the high impact of the environment on canaryseed grain yield (May et al., 2012a). In the present thesis it has been shown that delayed seeding of canaryseed cultivars with a putative vernalization requirement (Chapter 4) delayed their phenological development and caused plant morphological changes. Consequently, particular phenological phases closely related to grain yield production, such as those of stem elongation and grain filling, were possibly C-source limited (Chapter 6).

At high latitudes, rain-fed temperate cereal crops (ie, wheat, barley and oat) have relatively low green leaf area indices (GLAI) values, especially with low nitrogen fertilizer application rates. These, combined with lower solar radiation levels from the middle of the summer onwards, do not allow for high cumulative intercepted photosynthetically active radiation (CIPAR). Thus, lower biomass production seems more related to relatively low IPAR than to radiation use efficiency (RUE), which generally has relatively higher values (Muurinen and Peltonen-Sainio, 2006). In other environments, stress-induced biomass reductions are mainly due to reductions in GLAI (eg, in barley) or in RUE (eg, in triticale) but if stress commences early in crop development, biomass may be negatively affected by reductions in both IPAR and RUE (Fukai, 1995; Giunta and Motzo, 2004; Jamieson et al., 1995b; Estrada-Campuzano et al., 2012).

Temperate cereal response to vernalization and/or photoperiod often result in changes in water availability and to the incident and intercepted solar radiation (eg, Steinfort et al., 2017). Water availability likely affects the crop leaf canopy of temperate cereals (Muurinen and Peltonen-Sainio, 2006) via individual leaf cell growth and expansion. In turn, incident and intercepted solar radiation may change according to the genotype life cycle or individual phase duration and morphological responses.

Being the second determinant of biomass production, RUE is a physiological characteristic used in the interpretation of crop response to abiotic environment, genetic variation and crop management practices. Differences in RUE between small grain temperate cereals species or cultivars within species have been reported in the literature but the magnitude differs based on the phenological phases (Green, 1989; Calderini et al., 1997), year of cultivar release (Calderini

et al., 1997; Muurinen and Peltonen-Sainio, 2006), phenological development (Estrada-Campuzano et al., 2012) and the latitude. At high latitudes, differences are relatively small and often statistically non-significant (Kemanian et al., 2004; Muurinen and Peltonen-Sainio, 2006). Information in the literature on the effect of SD on RUE of temperate cereals is scarce and inconclusive (eg, Miralles and Slafer, 1997 for wheat; Kemanian et al., 2004 for barley).

Canaryseed plant grain yield was significantly reduced with delayed seeding (Chapter 6). In Mediterranean-type environments, when higher amounts of rainfall occur prior to anthesis, relatively high grain yields are produced (Austin et al., 1998a and b; Cossani et al., 2009). However, when drought stress is imposed which in such environments often coincides with the grain filling period, then grain yield and Harvest Index (HI) are both reduced. In contrast, at high latitudes, rain-fed temperate cereal crops show increased HIs with early season drought and low vegetative biomass production whereas potential later precipitation during the grain filling period results in high grain weight relative to total biomass, increasing the HI but not necessarily the grain yield (Peltonen-Sainio et al., 2008).

Under optimal growing conditions, SDs have little effect on HI of crops (Hay, 1995). However, when stress is imposed, HI can be negatively correlated to longer growing periods and later maturity in wheat due to frost or lodging (Stapper and Fischer, 1990) or stress during, or near, the end of the growing season (Hucl and Baker, 1987). Reduced HI in cereals related to water stress and delayed phenological development as a result of contrasting SDs have been reported for a series of temperate cereals such as spring wheat (Hucl and Baker, 1987), durum wheat (Giunta et al., 1993) and triticale (Campuzano et al., 2012). Optimal or recommended SDs normally result in better yields than late SDs (eg, Lanning et al., 2012). In contrast, later SDs delay the fulfillment of vernalization requirements of vernalization- and/or photoperiod-sensitive genotypes (Steinfort et al., 2017). This often coincides with lower pre-anthesis photothermal quotients, which have negative effects on grain yield and yield components (eg, Rawson and Bagga, 1979; Fischer, 1985; Savin and Slafer, 1991).

Grain yield of temperate cereals has been extensively studied by means of its numerical components (eg, inflorescence number per unit of cultivated area, seed number per unit area and per inflorescence, and average seed weight) (eg, Fischer and Mauer, 1978). Under Mediterranean-type environments, the grain yield component with the largest sensitivity is the grain number per unit of cultivated area as reported for a series of temperate cereal species (Fischer and Mauer, 1978; Cossani et al., 2009; Francia et al., 2011; Estrada-Campuzano et al., 2012). Number of spikes is also affected (Prado et al., 2017; Giunta et al., 1993; Estrada-Campuzano et al., 2012), though not as commonly in barley, especially two-row barley, due to

its relatively lower plasticity (García del Moral et al., 2003). If water stress is imposed in the post-anthesis period during the process of grain filling, grain weight is reduced, mainly depending on the level of the stress (Fischer and Mauer, 1978; Estrada-Campuzano et al., 2012). Grain weight is also slightly reduced with increased yields which often coincide with higher grain number per unit land area at higher levels of water availability (Siddique et al., 1989; Slafer and Andrade, 1993; Slafer et al., 1996).

The objective of this study was i) to determine if the reduced grain yield of canaryseed that is related to its putative vernalization requirement is associated with differences in crop biomass production and its components (CIPAR and RUE) or the dry matter distribution to seed yield (HI), ii) to simultaneously compare canaryseed response to environmental conditions with that of two other temperate cereal species with no or minimal vernalization requirements and iii) to investigate genotypic variability for crop biomass production and its distribution to the harvestable product among three canaryseed cultivars.

7.2 Materials and methods

For information on plant material, growing conditions and experimental setup refer to the sections 6.2.1, 6.2.2 and 6.2.3, respectively.

7.2.1 Observations and estimates

Data on grain yield characteristics are based on the experiments carried out in all three years, however data on leaf canopy, intercepted radiation, radiation use efficiency and crop growth are based on the experiments conducted in 2013 and 2014.

The number of seedlings per sub-plot were counted at crop emergence (for the first two sub-plots harvested) or start of tillering phase (for the remaining seven sub-plots).

For information on the types of measurements refer to section 6.2.4. Regarding the weekly series destructive harvests, all seedlings per sub-plot were harvested (cut at ground level) and green or portions of green leaf blades (without the sheaths) were used for the sub-plot leaf area determination as measured by means of a LI-3000C leaf area meter and a LI-3050A conveyor belt attached to the meter. Percentage of IPAR (%IPAR) was determined weekly as soon as substantial light interception by the crop stand occurred in the central sub-plot of all of the plots of three replications per block (seldom for fewer replications per block when weather conditions obstructed the in situ observation). Four, 10-cm apart individual measurements were taken at the bottom of the sub-plot canopy, perpendicularly oriented to the seedlings rows. Each measurement was conducted simultaneously with an observation at the top of the canopy at the end of the sub-plot using two LI-191SA line quantum sensors and a LI-1400 data logger on

clear sunny days between 12:00pm and 2:00pm. GLAI was estimated for all year × SD combinations except for the late seeding in 2014, in a weekly (occasionally 10-14 days apart) manner, seven times throughout the crop cycle in 2013 and six times in 2014, up to 10-15 days prior to crop physiological maturity. The light attenuation or extinction coefficient (k_L) was estimated by making use of the %IPAR and GLAI data for the early and late seeding in 2014 and 2013, respectively. Ideally, the light interception observations and the destructive harvests would have been conducted on the same day but that was not always possible due to the numerous overcast days during the months of May and June. Periodical destructive LAI measurements were subjected to non-linear regression analyses and the logistic function was fitted to the values in order to obtain estimates of GLAI for the respective dates of PAR interception measurements. Sometimes, weather conditions permitted destructive GLAI and PAR observations to be conducted on the same day. Four to six (four for wheat and oat cultivars seeded early in 2014, five for the canaryseed cultivars seeded early in 2014, and six for all cultivars seeded late in 2013) destructively and mathematically estimated GLAI values up to the booting stage (Zadoks et al., 1974) were used for simple linear regressions with PAR interception measurements and k_L was estimated for each cultivar seeded early and late based on the equation from Monsi and Saeki (2005) for IPAR:

$IPAR(\%)= 1 – \exp^{(-k_L \times LAI)}$ (Equation 7.1).

The overcast weather conditions present on several days in June (increased cumulative rainfall as shown in Figure 3.1, which agrees with longterm average precipitation in June) and July (scattered clouds around noon) of each year obstructed the conduction of several %IPAR measurements, which were limited from four to six per year × seeding date × cultivar × plot combination. These were supplemented by estimates of %IPAR based on the destructively estimated GLAI and the k_L estimates. A total number of six to 11 of %IPAR estimates (mathematically and in situ measurements), depending on the growth cycle of the treatments, were fitted with the logistic function in order to obtain daily estimates of the %IPAR of the treatments.

CIPAR estimates over the total growth cycle or for certain phenophases were generated using the daily %IPAR and the estimates of daily incoming solar radiation obtained from the Thornton-Running solar radiation prediction model (Ball et al., 2004) using weather data from two different nearby stations (the University of Saskatchewan Horticulture station for rainfall data in 2013 and 2014 and the Saskatchewan Research Council station for temperature data in 2013 and 2014).

With regards to the dry matter determination, after leaf area measurements, leaves of each sample were bulked with the remaining biomass per sub-plot and the samples were dried at 80°C for 48 hours or until stable dry weight was achieved (based on pilot trials). Dry weight was recorded to the second decimal place for the crop growth determination.

Anthesis was determined separately for each of the eight (two blocks × four replications $block^{-1}$) pre-assigned sub-plot per SD × cultivar treatment combinations based not only on the overall visual determination of the sub-plot but also on six individual seedlings as described in the section 6.2.4.3. As a result, destructive harvest at anthesis was not necessarily carried out on the same day for all eight plots per treatment.

A post-anthesis destructive harvest was carried out following the procedure described for anthesis when all anthers were dehisced, usually about five to seven days after the beginning of anthesis (or later for cultivar Keet, which had a high variation among individual seedlings), when the crop was at the early milk development stage (Zadoks et al., 1974).

At maturity, the central sub-plots were cut at ground level, the inflorescences were separated from the rest of the biomass, counted, and threshed and the grain was separated from chaff by means of a column with air-flow using different specifications for each cultivar in order to maintain the lowest grain loss with the chaff (always determined based on pilot trials). Samples were oven-dried as described above.

Procedures for GLAI and dry matter determination at anthesis and post-anthesis stages, as well as grain yield and dry matter at maturity, were as described for the repeated observations. Periodical destructive observations of the dry matter production were subjected to non-linear regression analyses using a flexible sigmoid function for determinate growth

$W = W_{max} (1 + (t_e - t) / (t_e - t_m)) (t / t_e)^{(t_e / t_e - t_m)}$ (Equation 7.2)

(Yin et al., 2003) where W is the crop dry weight and t is the time. The model returns estimates of the maximum crop growth rate, the time at which that was attained (t_m), the maximum crop dry weight and the time at which that it was reached (t_e) and so crop growth ceased.

Maximum relative growth rate (RGR_{max}) was estimated based on Baker and Gebeyehou (1982). Absolute crop growth rate (CGR) was estimated as the slope of the relationship of the cumulative crop dry matter against time starting no earlier than four weeks after seeding until the harvest event at post-anthesis. Simple linear regression analyses per plot between the destructively measured crop dry weight and the CIPAR by the crop canopy were conducted in order to obtain an estimate of RUE of the total growth cycle (crop emergence to physiological maturity subscripted as E-M). Separate regressions were conducted for the estimation of RUE

for the periods corresponding to pre- and post-anthesis (crop emergence to anthesis and from anthesis to physiological maturity subscripted as E-A and A-M, respectively).

7.2.2 Data analysis

For data analysis refer to section 5.2.5.

7.3 Results

7.3.1 Biomass production and its components (CIPAR and RUE)

7.3.1.1 Crop growth characteristics

Crop growth duration of canaryseed cultivars across year × SD combinations (hereafter the term "environments" will be used) was estimated from 1.3 to 9.4 and from 1.8 to 13.1 days longer compared to that of wheat and oat, respectively (Appendix 19). This is likely related to the delayed anthesis of canaryseed relative to wheat and oat (Appendix 21) as shown in Chapter 6. However, average crop growth rate of canaryseed cultivars was from 0.1 to 3.3 and from 3.2 to 6.9 g of dry matter m^{-2} d^{-1} lower compared to the corresponding wheat and oat values, respectively.

7.3.1.2 Associations between biomass and its components

In general, $Biomass_{E\text{-}M}$ was shown to be associated to $CIPAR_{E\_M}$ for all three species seeded in 2013 and 2014 (Figure 7.1). Relationships between $CIPAR_{E\_M}$ and the $Biomass_{E\text{-}M}$ were significant ($P \leq 0.014$) for all three species and relatively stronger for wheat and oat compared to canaryseed. On the other hand, the relationship between RUE_{E_M} and $Biomass_{E\text{-}M}$ was relatively weaker or even non-existent. The reason for the moderate association of Biomass with CIPAR in canaryseed cultivars was the weak and non-significant relationship between $CIPAR_{E\_M}$ and $Biomass_{E\text{-}M}$ with late seeding (Adj-r^2=0.26; P>0.1).

$Biomass_{E\_A}$, as for the total crop life cycle, was more associated with $CIPAR_{E\_A}$ than with the RUE_{E_A} for all three species (Figures 7.1 and 7.2). The relationship between $Biomass_{E\text{-}A}$ and $CIPAR_{E\_A}$, when considering all three canaryseed cultivars in all environments, was strongly significant ($P < 0.001$) but relatively weaker (r^2=0.40) compared to the corresponding relationship for early seeding only (Figure 7.2). This was likely due to the lower RUE_{E_A} of canaryseed cultivars with later seeding.

$Biomass_{A\text{-}M}$ of canaryseed cultivars, in contrast to $Biomass_{E\text{-}M}$ and $Biomass_{E\_A}$, was relatively poorly associated with $CIPAR_{A\_M}$. It was, however, associated with RUE_{A_M} (Figures 7.1 and 7.2). That was not the case for the other two species which in the post-anthesis phase,

alike the pre-anthesis phase showed closer association of the $Biomass_{A\_M}$ with $CIPAR_{A\_M}$ and not with RUE_{A_M}.

7.3.1.3 Seeding date and cultivar effects on biomass and its components

SD affected the $biomass_{E\text{-}M}$ for all cultivars in 2012 and 2014 with exception of CDC Togo (Table 7.1 and 7.4). However, the differences in biomass produced by the five cultivars across environments was dependent on the year of testing. Although $biomass_{E\text{-}M}$ was similar or lower with late compared to early seeding in 2013 and 2014, in 2012 all five cultivars produced more $biomass_{E\text{-}M}$ with later seeding. Canaryseed cultivar $biomass_{E\text{-}M}$ ranged from 647 to 1019 g m^{-2} across environments (1.6-fold variation). Wheat and oat ranged from 688 to 1071 and 920 to 1227 Kg ha^{-1}, respectively (1.6-fold and 1.3-fold difference, respectively).

Differences between glabrous canaryseed cultivars were inconsistent and non-significant. Pubescent cultivar Keet produced slightly but non-significantly higher biomass than the glabrous cultivars with both early and late seeding. That was due to higher $CIPAR_{E\_M}$ in three out of four environments, most likely due to the longer duration in chronological and thermal time (Tt) that Keet plants required from emergence to anthesis and therefore to maturity (Chapter 6). Canaryseed cultivars, in general, produced significantly ($P < 0.05$) less biomass compared to oat, mainly due to lower RUE_{E_M}. Differences with wheat, however, were smaller, inconsistent and non-significant (Table 7.1).

Cultivars differed significantly ($P < 0.05$) in $CIPAR_{E\_M}$ in two out of four environments (Table 7.1). Keet usually had higher $CIPAR_{E\_M}$ compared to wheat but differences with the glabrous canaryseed cultivars and oat were relatively small and insignificant. For the glabrous canaryseed cultivars that did intercept similar and non-significantly different PAR, the relationship with wheat and oat was inconsistent.

Generally, SD did have an impact on RUE_{E_M} for all five cultivars as they showed lower RUE_{E_M} with late seeding. Differences in RUE_{E_M} between SDs were significant ($P < 0.05$) in 2013 for canaryseed and in 2014 for wheat and oat. Canaryseed cultivar RUE_{E_M} ranged from 1.68 to 2.23 g MJ^{-1} across environments. Wheat and oat cultivars RUE_{E_M} ranged from 1.93 to 2.22 and 1.99 to 2.54 across environments, respectively, showing higher mean values and slightly lower variability than those shown by the canaryseed cultivars (Table 7.1). Cultivar effect on RUE_{E_M} was significant ($P < 0.05$) in three out of four year × cultivar combinations. In general, canaryseed cultivars had lower RUE_{E_M} compared to oat and similar or lower compared to wheat. Differences in the extreme RUE_{E_M} means between canaryseed and the

other two species ranged from 0.33 to 0.74 MJ m^{-2}. These values appeared in 2013 at both the early and late seeding, respectively, as the RUE_{E_M} differences in 2014 were smaller.

Canaryseed cultivars produced similar $Biomass_{E\text{-}A}$ to that of wheat and oat at anthesis when averaged over environments. That was the result of slightly higher $CIPAR_{E\_A}$ and slightly lower RUE_{E_A} of canaryseed relative to the other crop species. The slightly higher $CIPAR_{E\_A}$ of canaryseed cultivars, with Keet showing the highest one, was likely due to their relatively longer duration from emergence to anthesis, when averaged over environments (Chapter 6).

The variation in $Biomass_{A\_M}$ of canaryseed cultivars across environments was higher than that shown in the pre-anthesis phase (Table 7.2). Cultivar differences were significant ($P < 0.05$) in most environments. Later SDs resulted in mainly non-significantly reduced biomass. This was due to lower RUE_{A_M} in 2013 and due to lower $CIPAR_{E\_M}$ in 2014. For wheat, differences between environments were accompanied by similar differences in both $CIPAR_{E\_M}$ and $RUE_{A\_M,}$ and differences for oat were minor.

Table 7.1. Biomass, cumulative intercepted photosynthetically active aradiation (CIPAR) and radiation use efficiency (RUE) for three canaryseed, one spring wheat and one oat cultivar seeded on two dates in 2013 and 2014.

Cultivar	Stat.An.[1]	2013		Sign.[4]	2014		Sign.
		Early	Late		Early	Late	
		Biomass (g m^{-2})					
Togo		780b	718b	Ns[5]	912d	827bc	ns
Bastia		767b	735b	ns	953cd	770cd	**
Keet		849ab	772b	ns	1019bc	894ab	+
Barrie		817b	801b	ns	1064b	688d	***
Morrison		920a	1027a	ns	1209a	960a	**
	SEM[2]	43.7	36.0		44.3	38.6	
	Sign.[3]	*	***		***	***	
		CIPAR (MJ m^{-2})					
Togo		385b	441a	+	487a	439ab	ns
Bastia		396ab	452a	ns	489a	404bc	**
Keet		437a	489a	**	509a	479a	ns
Barrie		382b	428a	+	493a	367c	***
Morrison		413ab	463a	*	520a	447ab	**
	SEM	14.9	21.7		14.7	13.6	
	Sign.	*	ns		ns	**	
		RUE (g MJ^{-1})					
Togo		2.23ab	1.68c	***	2.03b	1.95a	ns
Bastia		2.15b	1.70c	*	2.09b	2.03a	ns
Keet		2.08b	1.74bc	*	2.09ab	1.90a	+
Barrie		2.22ab	2.07b	ns	2.20ab	1.93a	**
Morrison		2.41a	2.42a	ns	2.54a	1.99a	**
	SEM	0.010	0.096		0.114	0.078	
	Sign.	*	***		*	ns	

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Significance of the statistical test between seeding date means within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [5]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. Standard error in brackets. Mean values and means separation are based on three replications from each of the two blocks per year × seeding date × cultivar combination.

Table 7.2. Biomass, cumulative intercepted photosynthetically active radiation (CIPAR) and radiation use efficiency (RUE) from emergence to anthesis (E_A) and from anthesis to maturity (A_M) for three canaryseed, one spring wheat and one oat cultivar seeded on two in 2013 and 2014.

Cultivar	Stat.An.[1]			Sign.[4]			Sign.
		2013			2014		
		Early	Late		Early	Late	
				$Biomass_{E\_A}$ (g m^{-2})			
Togo		412a	438a	+[5]	565a	549a	ns
Bastia		441a	466a	ns	518a	394b	*
Keet		463a	565a	ns	590a	534ab	ns
Barrie		517a	481a	ns	625a	393b	**
Morrison		454a	527a	ns	654a	423ab	*
	SEM[2]	29.4	43.7		55.1	40.3	
	Sign.[3]	+	ns		+	**	
				$CIPAR_{E\_A}$ (MJ m^{-2})			
Togo		169b	242b	***	262a	259ab	ns
Bastia		181b	245b	**	269a	208bc	***
Keet		202a	310a	***	288a	296a	ns
Barrie		202a	225bc	*	271a	196c	**
Morrison		183b	203c	*	260a	216bc	**
	SEM	5.2	11.8		12.5	14.6	
	Sign.	***	***		ns	***	
				RUE_{E_A} (g MJ^{-1})			
Togo		2.45a	1.72a	ns	2.20a	2.06a	ns
Bastia		2.47a	1.93a	*	2.01a	1.82a	ns
Keet		2.31a	1.78a	*	2.04a	1.70a	+
Barrie		2.43a	2.12a	*	2.26a	1.90a	ns
Morrison		2.52a	2.37a	ns	2.61a	1.73a	***
	SEM	0.147	0.165		0.172	0.149	
	Sign.	ns	+		ns	ns	
				$Biomass_{A\_M}$ (g m^{-2})			
Togo		404ab	296bc	ns	366	292	ns
Bastia		363b	266bc	+	465	379	ns
Keet		404ab	223c	*	453	384	ns
Barrie		284b	335b	ns	456	298	+
Morrison		512a	499a	ns	512	508	ns
	SEM	39.7	44.2		54.4	53.9	
	Sign.	**	**		ns	*	
				$CIPAR_{A\_M}$ (MJ m^{-2})			
Togo		216ab	199b	**	225a	180a	+
Bastia		215ab	207ab	ns	220a	196ab	ns
Keet		235a	179b	*	221a	182ab	ns
Barrie		180b	203ab	*	222a	171b	**
Morrison		231a	261a	ns	260a	231a	+
	SEM	11.5	14.5		12.9	13.6	
	Sign.	**	**		ns	*	
				RUE_{A_M} (g MJ^{-1})			
Togo		2.06a	1.33a	*	1.67a	1.63a	ns
Bastia		1.70a	1.19a	*	2.07a	2.15a	ns
Keet		1.74a	1.53a	ns	2.02a	2.24a	ns
Barrie		1.64a	1.84a	ns	2.08a	1.70a	ns
Morrison		2.25a	2.25a	ns	2.08a	2.28a	ns
	SEM	0.158	0.309		0.239	0.270	
	Sign.	+	ns		ns	+	

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Significance of the statistical test between seeding date means within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [5]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. Standard error in brackets. Mean values and means separation are based on three replications from each of the two blocks per year × seeding date × cultivar combination.

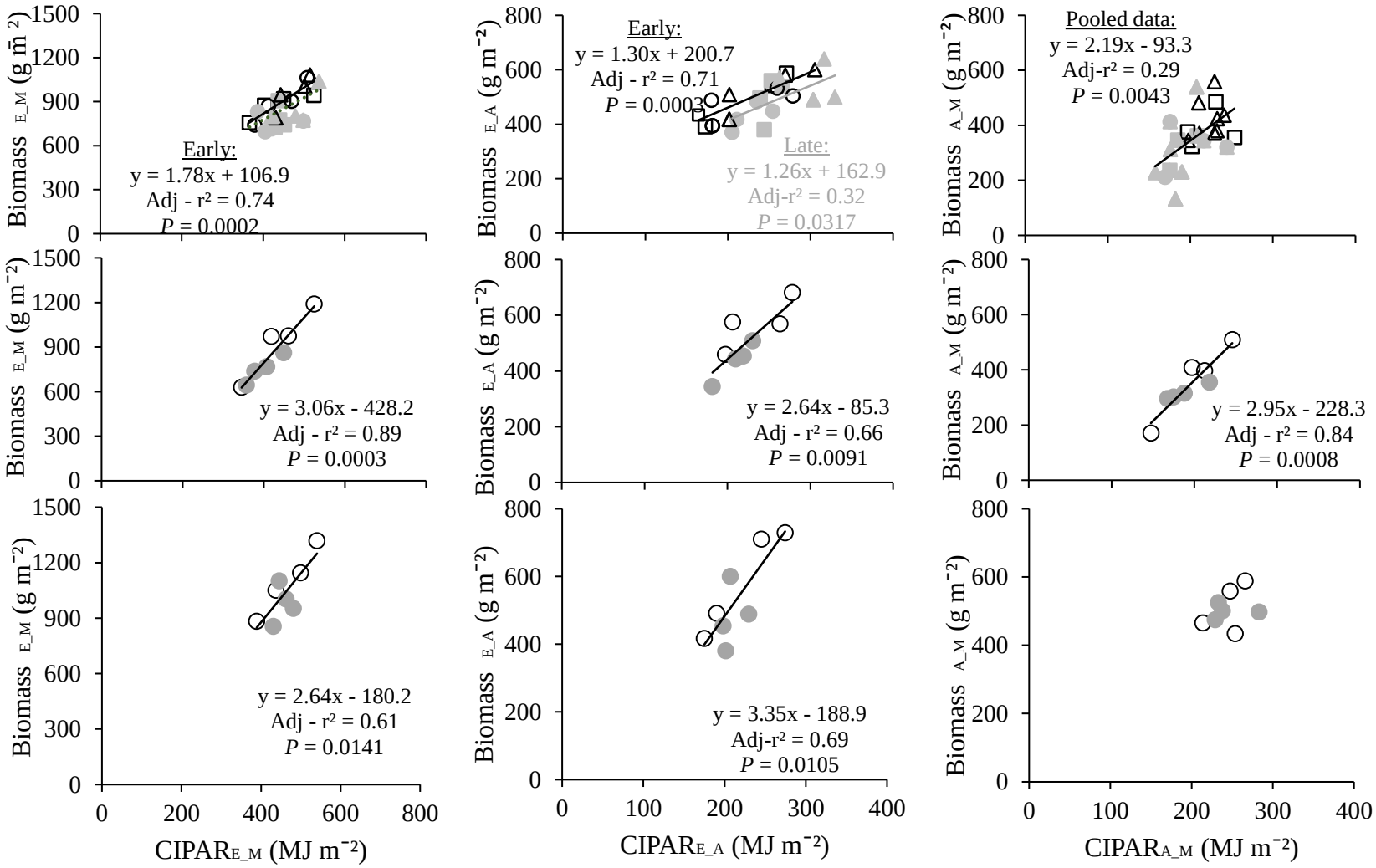

Figure 7.1. Above ground biomass versus the cumulative intercepted photosynthetically active radiation (CIPAR) from crop emergence to maturity (left column of panels), from crop emergence to anthesis (middle column of panels) and from anthesis to physiological maturity (right column of panels) for the canaryseed cultivar CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) (top row of panels), a spring wheat (middle row of panels) and an oat cultivar (bottom row of panels) seeded early (open symbols) and late (grey-closed symbols) in 2013 and 2014.

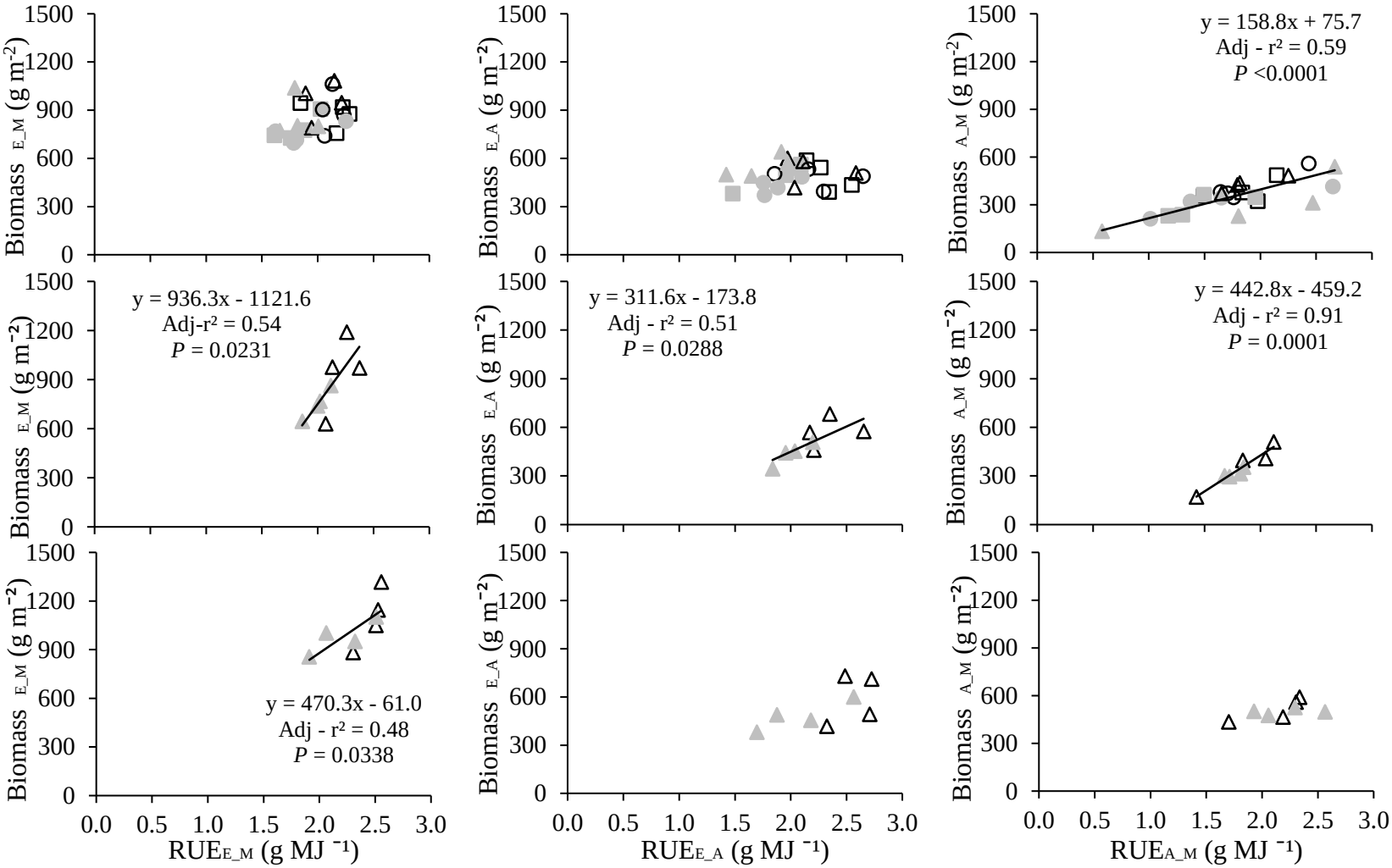

Figure 7.2. Above ground biomass versus the radiation use efficiency (RUE) from crop emergence to maturity (left column of panels), from crop emergence to anthesis (middle column of panels) and from anthesis to physiological maturity (right column of panels) for the canaryseed cultivar CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) (top row of panels), a spring wheat (middle row of panels) and an oat cultivar (bottom row of panels) seeded early (open symbols) and late (grey-closed symbols) in 2013 and 2014.

Glabrous canaryseed cultivars had a similar GLAI development patterns between SDs in 2013 but late seeded crops showed substantially higher maximum values (Figure 7.3). In contrast, in 2014, maximum GLAI values of glabrous canaryseed cultivars were similar between the SDs while late seeded crops showed a delay in GLAI development.

Maximum GLAI values of glabrous canaryseed cultivars with early seeding in 2013 were lower compared to those of wheat, oat and the pubescent canaryseed cultivar. However, the corresponding values in 2014 were similar, with oat being the only cultivar that reached higher values compared to the other four cultivars. In contrast, maximum GLAI values of all late seeded canaryseed cultivars were similar to those reached by wheat and oat, in both years.

k_L was estimated for each of the five cultivars in two out of four environments. All three canaryseed cultivars had higher k_L compared to wheat and oat, although differences were significant ($P < 0.05$) only between canaryseed cultivars and wheat in 2013. Averaged canaryseed k_L values, over the three cultivars and the two SDs were substantially higher than those of wheat and oat (Table 7.3). k_L differences between SDs were relatively small and significant ($P < 0.05$) only for Keet and AC Barrie. Differences in the k_L for these two cultivars between SDs resulted in differences in critical GLAI values. Nevertheless, GLAI of all five cultivars were well below their calculated critical values throughout the crop's life cycle, especially in 2013. This resulted in %IPAR values that were below the critical ones, which is shown by the scatter plot of the %IPAR versus the GLAI for each crop species separately (Figure 7.5). Maximum wheat %IPAR was relatively lower than that of the other two crop species regardless of the SD, likely due to the lower k_L values.

Table 7.3. Light attenuation coefficient (k_L) for three canaryseed, one spring wheat and one oat cultivar when seeded early and late in 2014 and 2013, respectively.

Cultivar	Stat. An.[1]	Early			Late			Significance of seeding date effect
			Regression			Regression		
		k_L	*P*-value	Adj-r^2	k_L	*P*-value	Adj-r^2	
Togo		0.49(0.069)a	***	≥0.98	0.44(0.019)ab	***	≥0.98	ns[4]
Bastia		0.47(0.013)a	***	≥0.96	0.49(0.031)a	**	≥0.92	ns
Keet		0.55(0.015)a	***	≥0.95	0.47(0.003)a	***	≥0.97	*
Barrie		0.36(0.007)a	***	≥0.96	0.33(0.001)b	***	≥0.97	*
Morrison		0.42(0.045)a	***	≥0.97	0.41(0.029)ab	**	≥0.93	ns
	SEM[2]	0.038			0.021			
	Sign.[3]	+			*			

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination Mean separations were conducted by Tukey's tests. [4]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. Standard error in brackets. Mean values and means separation are based on three replications from each of the two blocks per year × seeding date × cultivar combination.

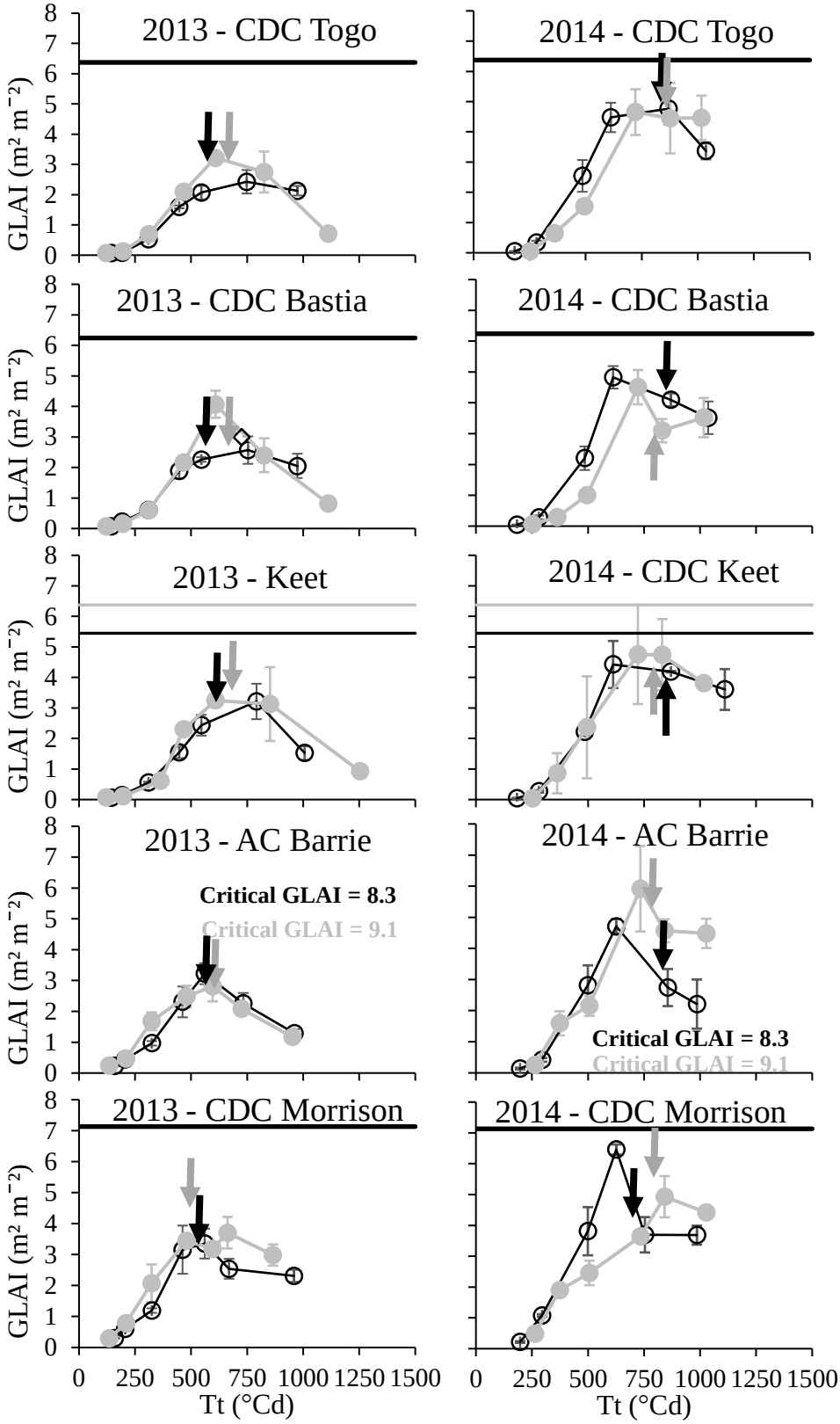

Figure 7.3. Green leaf area index (GLAI) versus the thermal time from crop emergence (Tt) for three canaryseed, one wheat and one oat cultivar seeded early (black symbols and curve) and late (grey symbols and curve). Thick and thin black and thin grey horizontal solid lines in individual panels denote the critical GLAI averaged over the two seeding dates, for the early and for the late seeding dates, respectively. Arrows indicate the Tt at main stem anthesis.

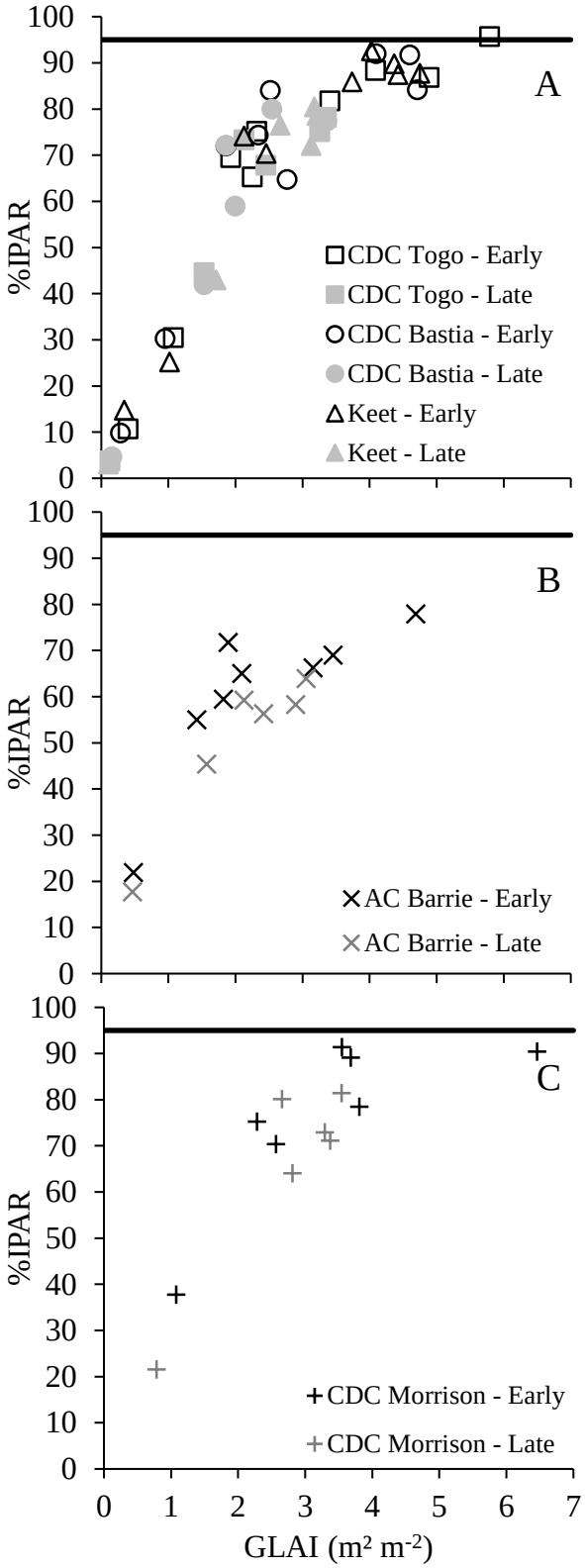

Figure 7.4. Percentage of intercepted photosynthetically active radiation (%IPAR) versus the green leaf area index (GLAI) for three canaryseed (A), one wheat (B) and one oat (C) cultivar seeded early (black symbols) and late (grey symbols). Thick black horizontal solid lines in individual panels denote the 95 %IPAR at critical GLAI.

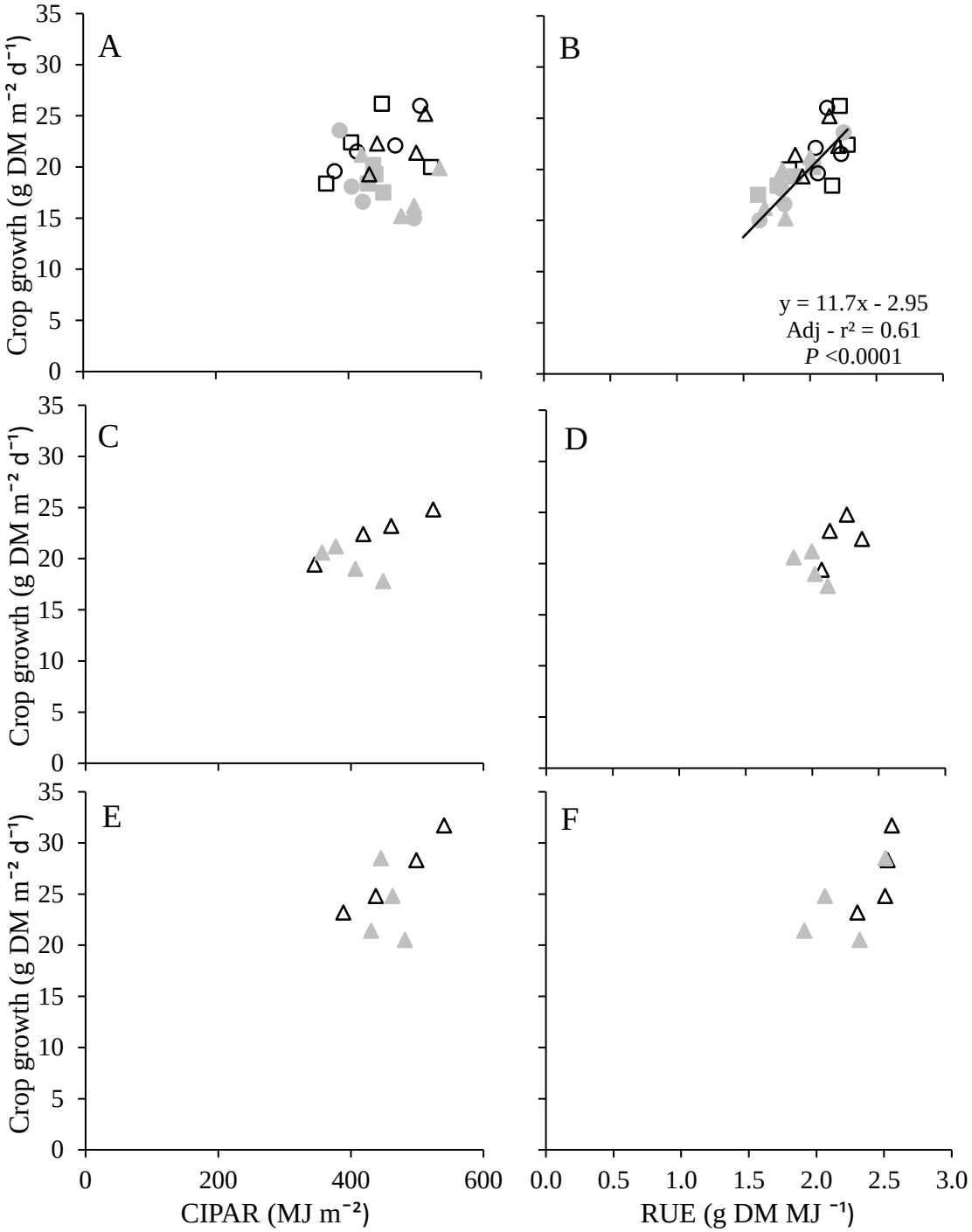

Figure 7.5. Crop growth versus the cumulative intercepted photosynthetically active radiation (CIPAR, panels A, C and E) and versus the radiation use efficiency (RUE, panels B, D and F) from crop emergence to physiological maturity for the canaryseed cultivars CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) (panels A and B), a spring wheat (panels C and D) and an oat cultivar (panels E and F) seeded early (open symbols) and late (grey-closed symbols) in 2013 and 2014.

7.3.2 Grain yield and its components

7.3.2.1 Associations between grain yield and its components

In general, grain yield was associated with $Biomass_{E\_M}$ for all three species. Considering all environments per crop species, the relationships between grain yield and $Biomass_{E\text{-}M}$ was relatively strong and highly significant ($P < 0.0001$) (Figures 7.7-A, C and E).

In contrast to $Biomass_{E\text{-}M}$, harvest index was associated with grain yield for canaryseed cultivars only and the relationship was highly significant ($P < 0.0001$) (Figure 7.7-B, D and F).

Grain yield of all three species was closely and highly significantly ($P < 0.0001$) associated with kernel number m^{-2} (Figure 7.8-A, C and E). The relationships for both wheat and oat showed a steeper slope, approximately five times higher than that for the canaryseed cultivars. Such a difference in slopes was exactly the difference between the kernel weight of the canaryseed cultivars and that of the other species when considering all environments (Table 7.5). On the other hand, kernel weight was associated with grain yield for wheat only (Figure 7.7- B, D and F). This relationship was distinct for the SDs while the intercept for the early seeding was higher, likely due to the clear SD effect on the kernel number per unit of cultivated area (Table 7.5).

The inflorescence HI of canaryseed cultivars partially explained the variation in kernel number m^{-2} (Figure 7.8) due to its close association with the kernel number $inflorescence^{-1}$ (Appendix 23). The same was not observed for oat and wheat. Although kernel number $inflorescence^{-1}$ moderately explained the variation in inflorescence HI, the latter was not associated with kernel number m^{-2}.

Despite the close association of canaryseed kernel number $inflorescence^{-1}$ with its HI (which in turn partially explained kernel number m^{-2} and grain yield), inflorescence number was not associated with kernel number m^{-2}, as might have been expected (Figure 7.8). There was a moderate negative relationship between the two variables when canaryseed cultivars were seeded early but no relationship was found when considering all environments. For wheat and oat cultivars, the relationship between inflorescence number m^{-2} and kernel number m^{-2} was not significant. The second component of kernel number m^{-2}, namely the kernel number $inflorescence^{-1}$, explained part of the variation in kernel number m^{-2} for oat and canaryseed (Figure 7.8).

Table 7.4. Grain yield, biomass and harvest index of three canaryseed, one spring wheat and one oat cultivar seeded on two dates in 2012, 2013 and 2014.

Cultivar	Stat. An.[1]	2012		Sign.[4]	2013		Sign.	2014		Sign.
		Early	Late		Early	Late		Early	Late	
					Grain yield (g m^{-2})					
Togo		136d	146d	ns[5]	185c	158c	*	242d	196d	*
Bastia		141d	166d	ns	181c	160c	+	255cd	206cd	**
Keet		199c	240c	+	226c	161c	*	295c	228bc	**
Barrie		362b	357b	ns	322b	306b	ns	389b	244b	***
Morrison		477a	538a	ns	404a	463a	+	537a	446a	**
	SEM[2]	17.8	13.0		16.7	13.0		15.3	11.3	
	Sign.[3]	***	***		***	***		***	***	
					Biomass (g m^{-2})					
Togo		647b	684c	ns	780b	718b	ns	912d	827bc	ns
Bastia		653b	783bc	*	767b	735b	ns	953cd	770cd	**
Keet		726b	938bc	**	849ab	772b	ns	1019bc	894ab	+
Barrie		967a	1073ab	*	817b	801b	ns	1064b	688d	***
Morrison		1017a	1217a	*	920a	1027a	ns	1209a	960a	**
	SEM	53.1	37.9		43.7	36.0		44.3	38.6	
	Sign.	***	***		*	***		***	***	
					Harvest index					
Togo		0.21d	0.21d	ns	0.24d	0.22c	*	0.27d	0.25d	*
Bastia		0.22d	0.21d	ns	0.24d	0.22c	**	0.27d	0.27c	ns
Keet		0.27c	0.26c	ns	0.27c	0.21c	***	0.29c	0.26cd	***
Barrie		0.37b	0.34b	*	0.40b	0.38b	*	0.36b	0.36b	ns
Morrison		0.46a	0.44a	ns	0.44a	0.45a	+	0.45a	0.47a	**
	SEM	0.008	0.010		0.004	0.005		0.005	0.005	
	Sign.	***	***		***	***		***	***	

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Significance of the statistical test between seeding date means within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [5]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. Standard error in brackets. Mean values and means separation are based on four replications from each of the two blocks per year × seeding date × cultivar combination.

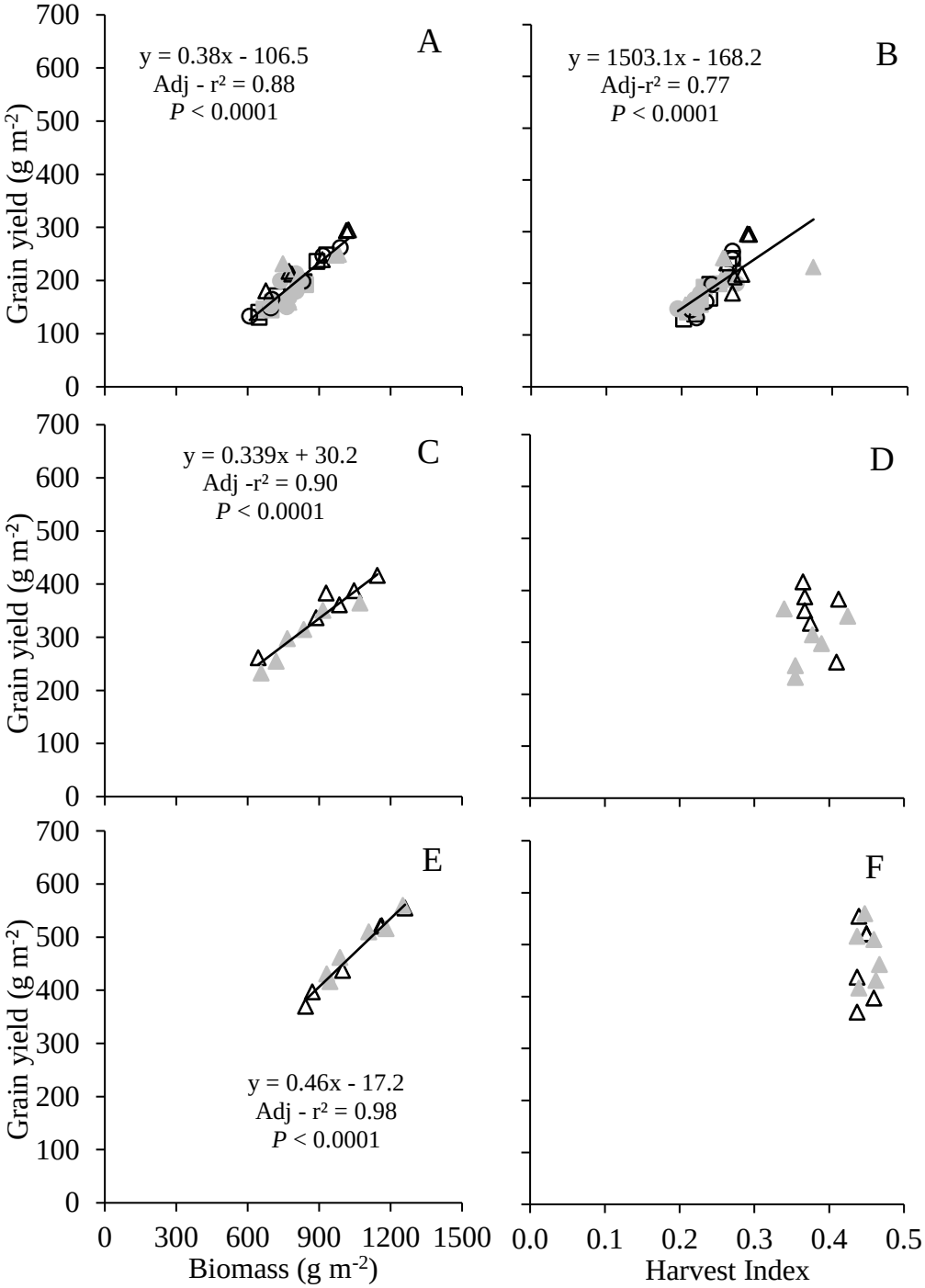

Figure 7.6. Grain yield versus the above ground biomass (panels A, C and E) and versus the harvest index (panels B, D and F) for the canaryseed cultivar CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) (panels A and B), a spring wheat (panels C and D) and an oat cultivar (panels E and F) seeded early (open symbols) and late (grey, closed symbols) in 2012, 2013 and 2014.

7.3.2.2 Associations between grain yield and its components

In general, SD significantly ($P < 0.1$) affected the grain yield of all three crop species in 2013 and 2014 but in 2012 differences were relatively small compared to the other years and

mainly non-significant (Table 7.4 and 7.5). Late seeding reduced the grain yield in all eight year × cultivar combinations of canaryseed and wheat cultivars (in six out of eight combinations the reduction was significant ($P < 0.05$)) in 2013 and 2014. However, late seeding did not have a clear effect on the grain yield of oat as the yield response was different among years. Only in 2014 did late seeding significantly ($P < 0.01$) reduce the grain yield of oat. Grain yield of canaryseed cultivars varied from 136 to 295 g m^2 among environments, showing an almost 2.2-fold variation. In contrast, grain yields of wheat and oat varied from 244 to 389 g m^2 (1.6-fold) and from 404 to 538 g m^2 (1.3-fold), respectively.

Cultivar effect on grain yield was significant ($P < 0.001$) in most environments as wheat and oat produced higher grain yields relative to all three canaryseed cultivars. Differences among canaryseed cultivars were significant ($P < 0.001$) only in 2012 and 2014. Keet was the cultivar that produced the highest grain yield of all three canaryseed cultivars with early seeding in all three years and the cultivar that showed the highest yield reduction when seeded late. Of the two glabrous canaryseed cultivars, CDC Bastia occasionally produced a higher grain yield than CDC Togo but the differences were usually small and not significant.

Late SDs generally significantly ($P < 0.05$) reduced the HI of canaryseed and wheat (Table 7.4). However, the reductions within years were smaller for wheat than for canaryseed cultivars. Differences in the HI of oat between SDs were small and usually not significant. As in the case of grain yield, the HI of Keet was higher compared to that of the glabrous cultivars when seeded early but had the largest difference between the SDs within years. The cultivar effect on HI was significant ($P < 0.001$) in all environments as both wheat and oat had higher HI compared to all three canaryseed cultivars. Differences between glabrous canaryseed cultivars were generally small and non-significant except with late seeding in 2014.

SD usually had a significant ($P < 0.05$) effect on kernel number m^{-2} (Table 7.5). Canaryseed and wheat had lower kernel number m^{-2} when seeded late. Oat kernel number was not consistently affected by SD, as was the case with oat grain yield and HI. The pubescent cultivar Keet, as with grain yield and HI, produced the highest kernel number m^{-2} compared to the two glabrous cultivars, when seeded early. In addition, the cultivar Keet had the highest reduction in kernel number m^{-2} when seeded late. The comparison between the two glabrous canaryseed cultivars showed that in contrast to their small and mainly non-significant differences in grain yield and HI, the kernel number of CDC Bastia was always higher than that of CDC Togo but the differences were non-significant. The differences in kernel number between the two glabrous canaryseed cultivars were counteracted by the higher kernel weight of CDC Togo relative to that of CDC Bastia, although the differences were non-significant (Table 7.5).

Differences in average kernel weight were also observed between the glabrous canaryseed cultivars and Keet, mainly due to the higher average kernel weight of CDC Togo relative to the other two canaryseed cultivars. However, those differences were again non-significant. The differences between environments within years and cultivars were smaller compared to the differences among canaryseed cultivars, except in 2012. Further, late seeding usually produced higher average kernel weight compared to the early seeding for all canaryseed cultivars, although the differences were not significant. Wheat and oat produced significantly ($P < 0.001$) lower kernel number and significantly ($P < 0.001$) higher average kernel weight compared to canaryseed cultivars, in all six environments.

In general, the effect of SD on the inflorescence HI was significant ($P < 0.001$) or nearly significant ($P < 0.1$) in many year × cultivar combinations (Table 7.6). Wheat and canaryseed had lower inflorescence HIs with late seeding, especially the cultivars Keet and CDC Togo. In contrast, oat had minimally reduced or even slightly increased inflorescence HI with late seeding.

SD usually significantly ($P < 0.001$) affected the inflorescence number m^{-2} of canaryseed between within-year environments (Table 7.6). However, the effect was not consistent across years. Wheat and oat, in turn, had lower variation in the inflorescence number compared to canaryseed. Of the canaryseed cultivars, the pubescent cultivar Keet had the lowest variation in the inflorescence number between within-year environments. Canaryseed cultivars produced significantly ($P < 0.01$) more inflorescences compared to wheat and/or oat in all environments.

The second determinant of kernel number m^{-2}, namely the kernel number inflorescence^{-1}, had up to a three-fold variation among environments (Table 7.6). Often the effects of the two main determinants of kernel number m^{-2} compensated each other for all three species but more often so for canaryseed. Wheat and oat had only half of the variation shown by the canaryseed cultivars.

Table 7.5. Grain yield, kernel weight and kernel number per unit of cultivated area from three canaryseed, one spring wheat and one oat cultivar seeded on two dates in 2012, 2013 and 2014.

Cultivar	Stat. An.[1]	2012		Sign.[4]	2013		Sign.	2014		Sign.
		Early	Late		Early	Late		Early	Late	
					Grain yield (g m^{-2})					
Togo		136d	146d	ns[5]	185c	158c	*	242d	196d	*
Bastia		141d	166d	ns	181c	160c	+	255cd	206cd	**
Keet		199c	240c	+	226c	161c	*	295c	228bc	**
Barrie		362b	357b	ns	322b	306b	ns	389b	244b	***
Morrison		477a	538a	ns	404a	463a	+	537a	446a	**
	SEM[2]	17.8	13.0		16.7	13.0		15.3	11.3	
	Sign.[3]	***	***		***	***		***	***	
					Kernel weight (mg)					
Togo		7.4b	7.9c	**	8.3c	8.4c	+	8.5c	8.3b	*
Bastia		6.8b	7.4c	***	7.5d	7.7d	***	7.5c	7.6b	ns
Keet		6.8b	7.5c	***	7.5d	7.7d	**	7.6c	7.6b	ns
Barrie		38.6a	42.8a	***	39.7b	41.5a	**	40.2b	38.9a	+
Morrison		38.3a	39.9b	**	45.0a	40.5b	***	42.4a	39.3a	***
	SEM	0.26	0.17		0.20	0.14		0.29	0.24	
	Sign.	***	***		***	***		***	***	
					Kernel number (x1000 m^{-2})					
Togo		18.29b	18.55bc	ns	22.32b	18.77b	*	28.58c	23.64b	*
Bastia		20.73b	22.62b	ns	24.17b	20.74a	*	33.85b	27.26a	**
Keet		28.97a	32.03a	ns	30.21a	21.05a	***	39.17a	29.87a	**
Barrie		9.46c	8.35d	*	8.19c	7.40d	ns	9.73d	6.19d	***
Morrison		11.99c	13.27cd	ns	8.96c	11.45c	**	12.67d	11.34c	+
	SEM	1.353	1.429		0.878	0.723		1.210	1.115	
	Sign.	***	***		***	***		***	***	

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Significance of the statistical test between seeding date means within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [5]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. Standard error in brackets. Mean values and means separation are based on four replications from each of the two blocks per year × seeding date × cultivar combination.

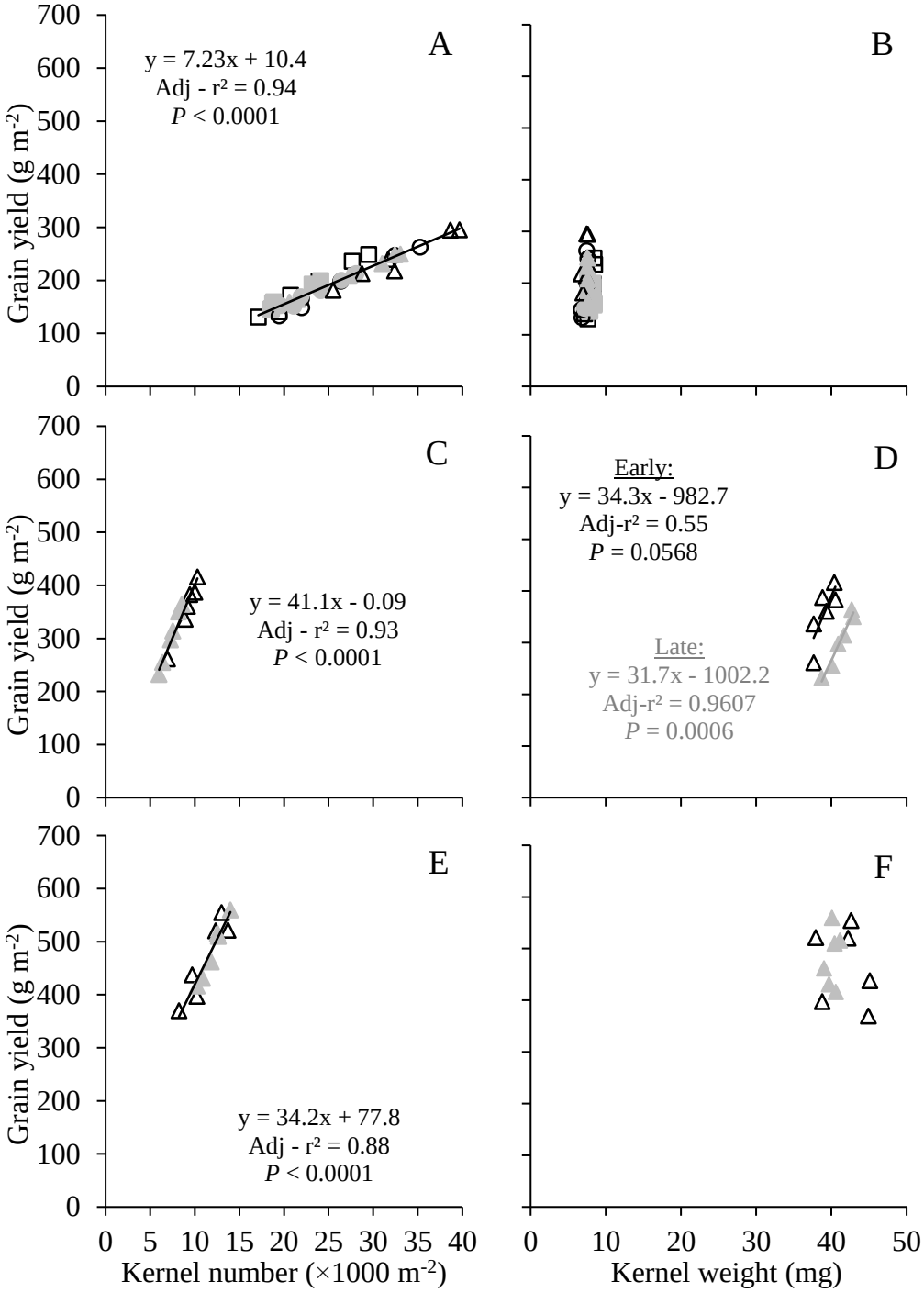

Figure 7.7. Grain yield versus the kernel number per unit of cultivated area (panels A, C and E) and versus the kernel weight (panels B, D and F) for the canaryseed cultivars CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) (panels A and B), for a spring wheat (panels C and D) and an oat cultivar (panels E and F) seeded early (open symbols) and late (grey, closed symbols) in 2012, 2013 and 2014.

Table 7.6. Grain yield characteristics for three canaryseed, one spring wheat and one oat cultivar seeded on two dates in 2012, 2013 and 2014.

Cultivar	Stat. An.[1]	2012		Sign.[4]	2013		Sign.	2014		Sign.
		Early	Late		Early	Late		Early	Late	
		Inflorescence number (m^{-2})								
Togo		751a	868a	ns[5]	626b	426a	***	493b	719a	**
Bastia		726ab	858a	*	770a	441a	***	553a	753a	**
Keet		620bc	654b	ns	548b	408a	***	511ab	522b	ns
Barrie		579c	560bc	ns	435c	391ab	ns	468b	404c	***
Morrison		395d	430c	ns	443c	340b	***	390c	391c	ns
	SEM[2]	38.7	37.1		25.3	18.3		16.3	25.5	
	Sign.[3]	***	***		***	**		***	***	
		Kernel number inflorescence $^{-1}$								
Togo		24.4b	21.7cd	ns	35.8b	44.4b	***	56.3b	34.7b	***
Bastia		29.1b	26.6bc	ns	33.4b	47.1ab	***	59.1b	36.4b	***
Keet		47.3a	49.0a	ns	53.2a	51.7a	ns	76.5a	57.1a	***
Barrie		16.6c	15.8d	ns	18.8c	21.0d	ns	20.9d	15.4d	***
Morrison		30.3b	31.1b	ns	20.2c	33.7c	***	32.6c	29.0c	*
	SEM	1.98	2.06		1.47	1.41		1.44	1.28	
	Sign.	***	***		***	***		***	***	
		Inflorescence harvest index								
Togo		0.57c	0.55e	ns	0.67d	0.65d	+	0.72d	0.65d	***
Bastia		0.59c	0.59d	ns	0.66d	0.65d	ns	0.74cd	0.67c	***
Keet		0.68b	0.72b	**	0.73c	0.70c	+	0.76bc	0.74b	+
Barrie		0.70b	0.67c	*	0.77b	0.74b	***	0.77b	0.70c	***
Morrison		0.84a	0.88a	ns	0.87a	0.86a	ns	0.89a	0.87a	***
	SEM	0.013	0.012		0.007	0.007		0.005	0.005	
	Sign.	***	***		***	***		***	***	

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [2] and [3] refer to the statistical test of the cultivar means within a year × seeding date combination [4] Significance of the statistical test between seeding date means within a year × cultivar combination. Mean separations were conducted by Tukey's tests. [5]ns, +, *, ** and *** used to denote that the statistical significance within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. Standard error in brackets. Mean values and means separation are based on four replications from each of the two blocks per year × seeding date × cultivar combination.

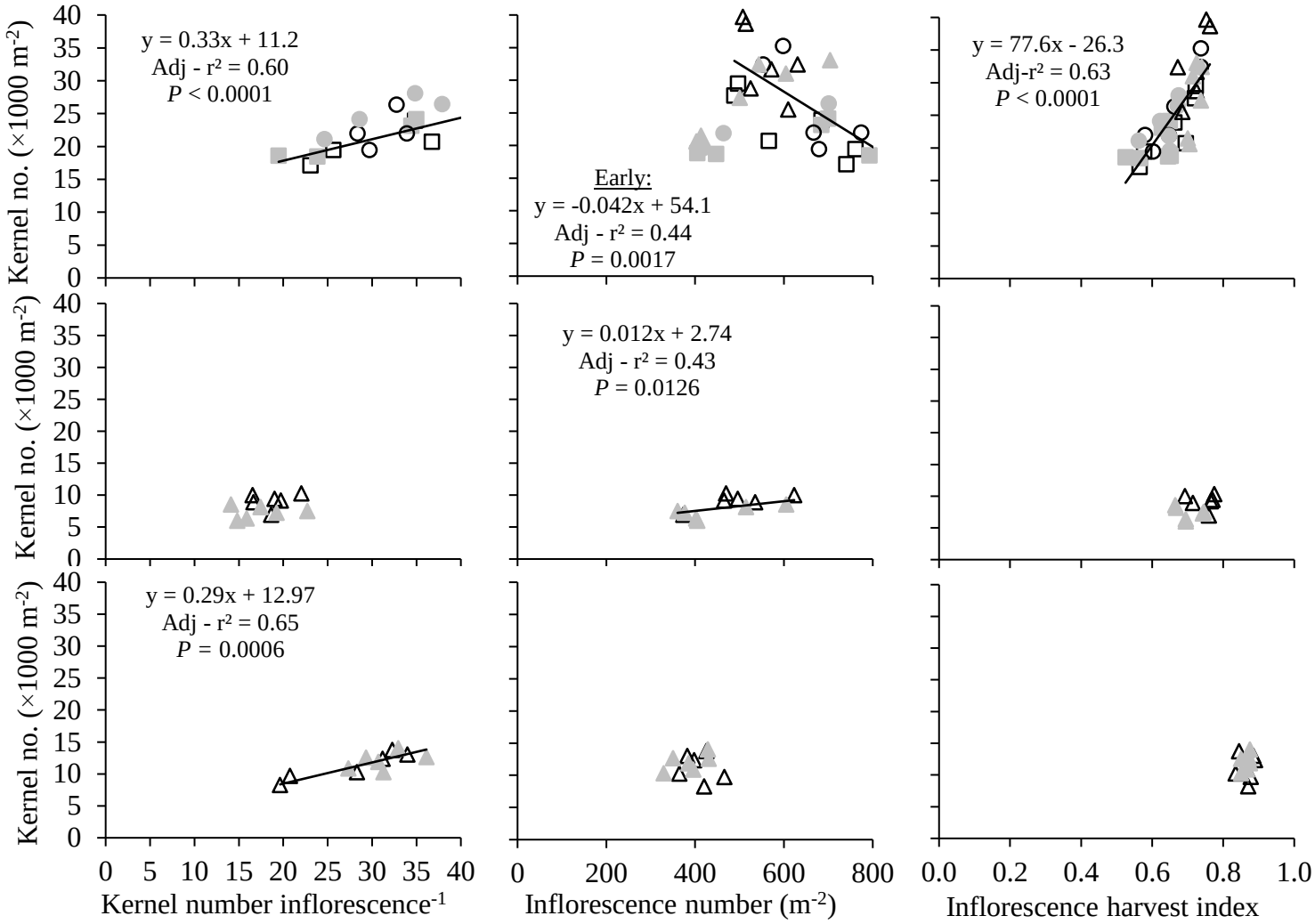

Figure 7.8. Kernel number versus the kernel number inflorescence^{-1} (left column of panels), versus the inflorescence number per unit of cultivated area (middle column of panels) and versus the inflorescence harvest index (right column of panels) for the canaryseed cultivars CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) (top row of panels), for a spring wheat (middle row of panels) and an oat cultivar (bottom row of panels) seeded early (open symbols) and late (grey-closed symbols) in 2012, 2013 and 2014.

7.4 Discussion

When canaryseed was tested under different environments with contrasting temperature, it exhibited genotypic variation for crop biomass, biomass components and, especially, for grain yield.

7.4.1 Biomass and its components

The range recorded in canaryseed crop biomass across environments (1.6-fold) was similar to wheat but higher compared to oat. Environmental impact (usually that of late seeding) on canaryseed biomass production was smaller compared to that on HI. This is in contrast to the eight-fold range in biomass accompanied by a three-fold range in HI reported by Bodega et al. (2003) in studies conducted in Argentina. In the present study, biomass reduction was mainly through reduced RUE, as will be discussed later, even though $CIPAR_{E\_A}$ also explained variation in biomass, especially with early seeding. Despite the delayed leaf canopy development (eg, late seeding in 2014) and the delayed and reduced maximum GLAI values (eg, both seeding dates in 2013) achieved by the canaryseed cultivars relative to wheat and oat, the CIPAR appeared to have been affected less than the RUE. This was likely the result of the relatively increased, in terms of Tt, pre-anthesis and crop life cycle duration of late seeded canaryseed and the few extra leaves formed (on the main stem) with both SDs, but especially with the late one. This likely improved their CIPAR (effect of environment on crop phenology – Chapter 6). However, potentially improved CIPAR for the reasons mentioned above were not necessarily associated with increased yield potential due to the small individual leaf area of the upper phytomers and the relatively shorter duration (especially with late seeding) of the phase from terminal spikelet to anthesis stage, when yield potential in cereals is formed.

There is currently a shortage of information on the growth and development pattern of canaryseed and the only reference to GLAI values are from Ford et al. (2001) who reported leaf area indices between 1.5 and 2.5 m^2 m^{-2}. Those values are similar but somewhat lower compared to the values recorded in the present study.

Despite the statistical non-significance in four out of six year × cultivar combinations, the lower $biomass_{E\text{-}M}$ production by the canaryseed cultivars with late seeding in 2013 and 2014 appeared to be the result of lower RUE_{E_M}. The impact of testing environments on RUE was more evident in the post-anthesis phase of the canaryseed crop cycle. Taking into account the shallow root system of canaryseed relative to wheat and oat, the impact on RUE is likely due to increasing frequency of water- and/or heat-stressful conditions, especially with late seeding. The impact of RUE_{E_M} on $Biomass_{E\text{-}M}$ is shown by the relatively strong and highly significant

($P < 0.0001$) relationship between the CGR_{E_M} and RUE_{E_M} (Figure 7.6). Interestingly, both wheat and oat showed weak (or even non-existent) relationships between CGR_{E_M} and each of the two components of $biomass_{E\text{-}M}$. This is likely due to the fact that differences between environments in CGR_{E_M} of both wheat and oat were relatively small, compared to those of the three canaryseed cultivars, and non-significant (Appendix 20). There is no published information on CGR of canaryseed to to facilitate comparisons. However, results of this study are consistent with results from experiments on the growth and biomass components of other temperate cereals, which reported reduced RUE due to water stress in barley (Jamieson et al., 1995b), in wheat and in triticale (Estrada-Campuzano et al., 2012).

The lower $Biomass_{E\text{-}M}$ due to lower RUE_{E_M} appears to differ from the results presented regarding biomass production and its components in section 7.3.1 where $Biomass_{E\text{-}M}$ was more associated with $CIPAR_{E\_M}$ than with RUE_{E_M}. That discrepancy is likely due to the differences in time or Tt duration in the pre-anthesis phase and the total crop cycle of canaryseed, especially the late seeded crops, as mentioned above and shown in this and the previous chapters (Appendix 19 and Appendix 21). Increased Tt to maturity was translated into increased $CIPAR_{E\_M}$. Although the latter was associated with $biomass_{E\text{-}M}$, the association was SD dependent due to reductions in RUE_{E_M}. Therefore, in environments similar to those encountered with the early seeding in this study, biomass would be more CIPAR dependent, especially in the pre-anthesis phase and assuming little or no reduction in RUE. In contrast, in environments similar to those encountered with the later seeding in this study where canaryseed would require longer Tt duration to reach maturity, biomass would be more associated with RUE than with CIPAR through reductions in CGR, as discussed above.

Environmental stress-free conditions and species have been reported to be main factors determining RUE (Kiniry et al., 1989). In contrast, variation in RUE of cereals has been reported for a series of species such as wheat (Muurinen and Peltonen-Sainio, 2006), barley (Gregory et al., 1992) and triticale (Estrada-Campuzano et al., 2012). RUE of canaryseed cultivars in the current study was reduced with late seeding but this was dependent on the year and cultivar. When considering the RUE of pre- and post-anthesis phases separately, differences in the RUE values were greater relative to the RUE_{E_M} values. It is possible that several factors related to crop canopy morphology might influence the RUE of canaryseed and the estimated values are the result of synergistic or counteracting effects on RUE. The higher k_L of canaryseed cultivars compared to the other two cereal crops might have allowed for lower levels of radiation to reach lower levels of the canopy. On the other hand, lower individual leaf area of the upper phytomers (Chapter 6) and/or the slightly lower k_L values with late seeding,

relative to early seeding (except from CDC Bastia), might have allowed for higher levels of radiation to reach deeper in the canopy. Different amounts of radiation reaching deeper layers in the canopy might have been used with different efficiency as described by Estrada-Campuzano et al. (2012). In addition, the proportion of covered soil by leaf canopy might have played a role in evapotranspiration and, in turn, in RUE. Thus, the high variation in canaryseed RUE values might have resulted from different factors influencing the RUE of the crops in contrasting directions. Higher GLAI values together with higher individual leaf areas of the top few leaves, and the lower k_L, might have resulted in the higher RUE values of wheat and oat.

7.4.2 Grain yield and yield components

When seeded early in the season, canaryseed cultivars produced higher grain yields, similar to those of wheat but still lower than those of oat. All three crop species had similar phenological development and CIPAR. Even under those circumstances, the variation in grain yield of canaryseed was greater than that recorded for wheat and oat. Canaryseed grain yield variation was approximately two-fold among early seeding and among environments. Such a variability was lower (Bodega et al., 2003; May et al., 2012a) or higher (Miller, 2000) compared to those reported and obtained from experiments conducted in different environments by means of different SDs. However, the variation recorded in grain yield is in agreement with May et al. (2012a) who concluded that environment has a large impact on canaryseed grain yield.

Considering all environments, canaryseed grain yield was correlated with above ground biomass and with HI. Biomass production and its components were discussed already. The HI, the distribution of the biomass to the seed yield, is largely reduced by water-stressful conditions during seed filling in cereals. Adjustment of phenological development of the crops is a strategy that has been implemented in order to avoid terminal drought (Araus et al., 2002 and references therein) and this strategy might be considered for improving canaryseed yield characteristics.

Phenological development (ie, time to anthesis) of canaryseed cultivars was usually delayed with delayed seeding (Chapter 6). Given that relatively lower amounts of rainfall were recorded towards the end of the growing season, this increased the potential for water-stressful conditions (Figure 7.1), especially for canaryseed given its shallow root system. Such water-stressful conditions coincided with later developmental phases, including stages near or after anthesis. Reduced HIs in cereals related to water stress and delayed phenological development have been reported for a series of crops such as spring wheat (Hucl and Baker, 1987), durum wheat (Giunta et al., 1993), triticale (Campuzano et al., 2012), rice (Jearakongman et al, 1995) and maize (Richards, 1996 and references therein). Thus, it is likely that delayed phenological

development of canaryseed negatively affected HIs with late seeding. In contrast to canaryseed, wheat and oat, which had faster development towards anthesis, also had smaller reductions of HI with late seeding.

The delayed phenological development of the pubescent cultivar Keet compared to CDC Bastia might account for differences observed between the two cultivars. Furthermore, Keet had larger reductions in HI compared to the two glabrous canaryseed cultivars. The harvest index of canaryseed cultivars was significantly lower compared to that of wheat and oat, similar to that reported by Cogliatti et al. (2011) but higher compared to that reported by Bodega et al. (1996).

Grain yield of canaryseed cultivars was strongly associated with grain number per unit of cultivated area but not with average kernel weight. This is in agreement with previous reports (Bodega et al., 2003; Cogliatti et al., 2011) on canaryseed and other temperate cereals such as barley, wheat and oat (Peltonen-Sainio et al., 2007). In addition, this agrees with the hypothesis that the grain yield of cereals is related to the capacity of the inflorescence to sink in the photo-assimilates (Boras et al., 2004). Nevertheless, the photo-assimilate availability during the seed-filling period should not be overlooked when considering canaryseed for reasons related to GLAI, individual leaf area of the upper phytomers, and the duration in Tt from terminal spikelet to anthesis, as discussed earlier in this chapter as well as in Chapter 6. Canaryseed grain yield was linearly correlated with the kernel number inflorescence^{-1}. Others have reported that kernel number inflorescence^{-1} was either inconsistently related to grain yield (Miller, 2000), linearly correlated to the number of seeds per unit of cultivated area and therefore to the yield (Bodega et al., 2003) or related to grain yield in a quadratic manner (May et al., 2012a). In all three studies that were mentioned above where different SDs were tested and were conducted either in the Canadian Prairies or in the Argentinian Pampas, the crops were exposed to increased temperatures with delayed seeding and long photoperiods. As for water availability, the crops experienced uneven precipitation patterns within years, either slightly or more intensively, with terminal drought being experienced in all years of the study (Miller, 2000) or in many site-years (May et al., 2012a).

In general, kernel number m^{-2} in canaryseed was not explained by the inflorescence number m^{-2}, in agreement with Bodega et al. (2003) A reason for the lack of association (at least for CDC Bastia) between the inflorescence number and kernel number m^{-2} was that many small panicles produced on small, usually higher ranked tillers, were counted together with larger panicles, from primary or lower ranked tillers, substantially contributing to grain yield. This increased the number of inflorescences m^{-2} but had little effect on the kernel number m^{-2}. This

was a pattern usually observed with CDC Bastia and to a lesser extent with the other two canaryseed cultivars.

7.5 Conclusions

This study demonstrated that contrasting SDs and canaryseed cultivars with a putative vernalization requirement caused variation in crop biomass, biomass components and grain yield. Canaryseed cultivars in general produced a biomass similar to that of wheat but smaller than that of oat. Canaryseed biomass with early SDs was more CIPAR dependent, especially in the pre-anthesis phase due to the delayed leaf canopy development and/or the delayed and reduced maximum GLAI values. In contrast, with later SDs, when canaryseed required longer Tt duration to reach maturity, biomass was more associated with RUE than with CIPAR through reductions in CGR. Considering all environments, canaryseed grain yield variation was best explained by changes in the HI than changes in the above-ground biomass. It is likely that the delayed phenological development of canaryseed negatively affected its HI with late seeding. In contrast to canaryseed, wheat and oat, which had faster development towards anthesis, also had smaller reductions in HI with late seeding. The grain yield of wheat and oat was therefore, determined by the crop biomass only, mainly due to CIPAR and to a lesser extent due to RUE. The delayed phenological development of the pubescent cultivar Keet compared to CDC Bastia might account for differences found between the two cultivars. Furthermore, Keet had larger reductions in HI compared to the two glabrous canaryseed cultivars. Grain yield of all three crop species was strongly associated with one of the main determinants, namely the grain number per unit of cultivated area.

Chapter 8 General discussion and conclusions

8.1 General discussion

Cnaryseed suffers from low and unstable grain yield when grown in Western Canada (Miller, 2000; May et al., 2012a) and Argentina (Bodega et al., 2003). Previous studies on SDs addressed the effect of the growing environment on canaryseed grain yield (Bodega et al., 2003; May et al., 2012a). Miller (2000) and Bodega et al. (2003) reported delayed anthesis and maturity due to delayed seeding. A correlation (r=0.66**) between decreased yields and delayed heading for early versus late seeded canaryseed experimental plots has been found (Hucl, personal communication, 2012).

8.1.1 An appropriate leaf-development scale for canaryseed

The use of the existing scales, often used in primary small grain temperate cereals, such as the Zadok's (Zadoks et al., 1974) and Haun's (Haun, 1973) scales, were either incontinuous and thus inappropriate for young seedling development (ie, Zadok's) or not known if appropriate for canaryseed due to its slightly different leaf appearance pattern (ie, Haun's). Therefore, a plant development scale was needed for comparison purposes while modifications of the Haun scale, based on the leaf lamina length of the youngest, the two youngest and all main stem leaves, generated alternative leaf-development-based scales that would more accurately estimate the phyllochron, the main stem leaf stage and the main stem actual leaf stage, respectively. Regression analyses and comparisons conducted between the modified Haun leaf scales returned highly significant (P<0.001) functions that explained more than 99% of the variation and revealed insignificant leaf stage differences. Thus, canaryseed leaf stage calculations are expected to be very similar using either of the leaf-based scales. Sonego et al. (2000) also demonstrated that despite the slightly different leaf appearance pattern of oat seedlings, relative to wheat, the Haun scale could be used to calculate leaf stages for oat plants with little error. It was concluded that despite the main stem leaf appearance overlapping in canaryseed cultivars, the common Haun scale or its modification based on the youngest leaf, is sufficient to determine canaryseed seedling leaf stages.

8.1.2 Putative low-temperature vernalization requirement of canaryseed

Temperate cereal plant responses to low-temperature vernalization, photoperiod and their interaction are phenotypically expressed via changes in the main stem FLN (Brooking et al., 1995; Mahfoozi et al., 2001a and b; Brooking and Jamieson, 2002). Canaryseed cultivar morphological responses to different air temperatures were therefore investigated under long

photoperiod in both, field and controlled-environment experiments and for first time documented. Canaryseed exhibited different main stem FLNs when grown in different environments, which primarily resulted from differences in air temperature due to different SDs. Canaryseed leaf-development pattern was evaluated among different SDs, in terms of the rate of elongated leaf primordium appearance. Differences in the elongated leaf primordium appearance rate among SDs were either small or did not correspond to those of the FLN. This is the first documented attempt where the elongated leaf primordium appearance rate was used to explain differences in the main stem FLN in temperate cereals. Based on the results, the hypothesis that the increased FLN of late seeded canaryseed is the product of its different leaf appearance pattern was disproved. In contrast, the $MHLS_{FI}$ and $MHLS_{TS}$ of field-grown seedlings from two canaryseed cultivars correlated with their main stem FLN. Such findings agree with those for wheat (Jamieson et al., 2007; Brown et al., 2013) and oat (Sonego et al., 2000), in the context of modeling time to anthesis thus modeling responses to vernalization and photoperiod. In addition, with exposure of canaryseed seedlings to low-temperature for up to 14 days, both canaryseed cultivars responded to low- (5°C) or relatively low-temperature (10°C) vernalizing treatments under the very long photoperiod by reducing the FLN as well as the $MHLS_{FI}$. Such a response agrees with the findings on the vernalization and photoperiod responses of wheat, as determined morphologically at its stem apex (Brooking, 1996; Robertson et al., 1996; Brooking and Jamieson, 2002). A putative low-temperature vernalization requirement of canaryseed cultivars was therefore concluded. Canaryseed FLN appeared sensitive to the plant physiological age, at the onset of vernalizing treatment which is in agreement with Wang et al. (1995) who concluded that 'the minimum vernalization duration required to reach a stage of vernalization insensitivity in wheat decreased as plant age at the onset of vernalization increased'. Canaryseed FLN appeared also sensitive to the post-vernalization growth conditions with higher air temperature (20 instead of 17°C) and longer photoperiod (20 instead of 17 h) increasing the FLN. This seems to be in disagreement with what Ream et al. (2014) reported on the grass species, brachypodium (*Brachypodium distachyon*) for which 16 or 20 h photoperiod during the post-vernalization plant growth period reduced both, days to flowering and FLN. The response of the canaryseed cultivars to the post-vernalizing growth conditions is a topic that requires further investigation.

8.1.3 Leaf appearance and tillering pattern

The canaryseed main stem leaf appearance rate changed during the expansion of the second leaf, while higher ranked leaves appeared faster compared to the preceding ones. That did not

appear to be the case for wheat and oat. Seed-stored reserves, leaf photo-assimilate supply and/or the prevailing photoperiod during the early seedling development were likely related to the canaryseed leaf appearance pattern. A similar phyllochron pattern has been reported for rapeseed when seeded on different dates and was related to the change in leaf morphology (Miralles et al., 2001). A change in the phyllochron has also been reported for other cereals such as wheat (Calderini et al., 1996; Jamieson et al., 1995a; Miralles and Richards, 2000; Miralles et al., 2001; Steinfort et al., 2017) and barley (Kirby et al., 1982; Miralles and Richards, 2000; Miralles et al., 2001; Abeledo et al., 2004) but was estimated to occur at higher ranked main stem leaves and it was inverted relative to that observed in canaryseed. The average phyllochron of the canaryseed cultivars appeared significantly higher with the late compared to the early and/or the very late SDs and shorter compared to that of wheat and oat. In wheat and barley, main stem phyllochron has been closely associated with tiller appearance (Klepper et al., 1982; Kirby et al., 1985) and these two characteristics of cereals are often studied together. The putative vernalization requirement of canaryseed (Chapter 4), and its potential relatively high importance of tiller-derived grain yield to the crop grain yield as implied by evidence from the study of May et al. (2012a) were hypothesized to be of interest in explaining the yield variability of the crop. Despite the shorter phyllochron of canaryseed cultivars relative to wheat and oat, canaryseed tiller appearance rates were similar or even slightly lower than those of wheat. This was due to the suppression of the first two or three primary tillers. Delayed and/or suppression of primary tillers has also been reported in spring and winter wheat cultivars and was related to unfavorable seedbeds (Klepper et al., 1982), increased seeding depth (Hucl and Baker, 1990) and the assimilation source to sink ratio of a plant (Evers et al., 2006). Higher FLN in canaryseed was accompanied by a delayed start of stem elongation. This is common in wheat while the start of stem elongation coincides with TS formation (Hay, 1999) which in turn is associated with FLN on the main stem (Jamieson et al., 2007; Brown et al., 2013). In canaryseed, the start of stem elongation was, in turn, negatively associated with the cessation of tiller appearance, in terms of Tt. This finding is the report of a temperate cereal crop for which a negative feedback mechanism could be involved in the regulation of tillering cessation. This is in contrast with what has been reported in wheat, where cessation of tiller appearance has been positively associated with stem elongation (Hay, 1999) and/or with threshold values of red:far red ratio and %IPAR under the crop leaf canopy (Evers et al., 2006; Alzueta et al., 2012). Indeed, in this present study the onset of tillering cessation in wheat and oat was more closely related to the %IPAR. Canaryseed also exhibited a delayed onset of tiller appearance compared to wheat and oat, especially when seeded late which is in agreement with findings on

wheat (Klepper et al., 1982; Hucl and Baker, 1990; Evers et al., 2006). Canaryseed onset and cessation of tiller appearance may potentially shorten the tiller appearance duration, which, together with a potential suppression of primary tillers, determines the number of tillers with a higher probability of reaching physiological maturity. Steinfort et al. (2017) also demonstrated that wheat isogenic lines differing in their vernalization and photoperiod sensitivity showed large variation in tiller number appearance and mortality.

8.1.4 Phenological development of canaryseed

Delayed seeding of canaryseed cultivars on the Canadian Prairies delayed the timing of key phenological stages, in terms of Tt, such as that of FI, TS formation and anthesis. The longer pre-anthesis phenological phases of canaryseed were mainly explained by the increased FLN, similar to other temperate cereals, and not by the changes in the average phyllochron. Delayed phenological development due to increased FLN as a result of different SDs has also been reported for wheat (Hay and Kirby, 1991; Miralles et al., 2001; Steinfort et al., 2017), barley (Miralles et al., 2001) and oat (Sonego et al., 2000). The length of the pre-anthesis phases with late SD was altered differentially among canaryseed cultivars. Steinfort et al. (2017) has shown differential response of pre-anthesis phases in wheat isogenic lines with differences in the allelic combination of loci that control the response to vernalization and photoperiod. In contrast, wheat and oat, generally differed little between the SDs with regards to these response variables. Therefore, the phenological response of canaryseed to SD was related to its putative vernalization requirement.

8.1.5 Main stem morphological characteristics and dry matter accumulation

The flag leaf area of late, compared to early seeded canaryseed cultivars was lower. The flag leaf area of early seeded canaryseed was positively and linearly associated with the main stem inflorescence grain yield. Similarly, Steinfort et al. (2017) reported that wheat isogenic lines with partially or unmet vernalization requirements had substantially lower flag leaf area, relative to those grown under short photoperiod and/or fulfilled vernalization requirement. Also, Simpson (1968) and Dimmock and Gooding (2002) reported positive associations between the grain yield and the photosynthetic area above the flag leaf node and the green flag leaf area duration, respectively in wheat. In addition, the duration of the stem elongation phase was negatively associated with the duration from emergence to TS. When canaryseed was seeded late, the main stem inflorescence, a large sink during the stem elongation phase, likely sunk relatively lower amounts of photo-assimilates compared to the early SDs. This is the first time for such an association to be reported in the literature of temperate cereals while Gonzalez-

Navarro et al. (2016) and Estrada-Campuzano et al. (2008) reported a slight positive relationship in wheat and lack of a relationship in triticale, respectively between the two phases. The relationship between those two phases found in canaryseed is likely of significance with regards to the contribution of main stem to the total grain yield and its variability. Considering that the main stem inflorescence dry weight at anthesis was related to its average growth rate and not to main stem height suggests that the former seems to have been more limited by source than by the competition with the main stem. This agrees with what is widely known in wheat, namely that its main stem inflorescence dry weight at anthesis is associated with the assimilate availability during its growth regardless of the factor causing the differences in the assimilate availability (ie, Fischer and Stockman, 1980; Fischer, 1985; Siddique et al., 1989; Fischer, 1993; Miralles et al., 2000). The putative C-source limitation of the main stem inflorescence is likely more pronounced with late seeded crops as a positive linear relationship was observed between the inflorescence dry weight at final harvest and its HI. In addition, the C-source limitation seems to hold during the grain filling period as well, given that main stem grain yield was positively and linearly associated with its average grain filling rate and not by the grain filling duration. It may be further supported by a potential mobilization of carbon reserves from tillers to the main stem when lower biomass of tiller stems at final harvest was found, relative to earlier phenological stages, especially when water deficit during the grain filling was increased (eg, 2013-late seeding) as Palta et al. (1994) reported in wheat. These main stem morphological and dry matter accumulation responses were mainly found in canaryseed or to a greater extent relative to wheat and oat.

8.1.6 Crop biomass, grain yield and their components

Canaryseed cultivars with a putative vernalization requirement (all three used in this study) seeded at different dates varied in crop biomass, biomass components and grain yield. Canaryseed grain yield was best explained by changes in the HI rather than by changes in the crop biomass. In general, canaryseed cultivars produced a biomass similar to wheat, lower than that of oat, and a lower grain yield as a result of a lower HI. In contrast, the grain yield of wheat and oat was determined by the crop biomass only, mainly due to CIPAR and to a lesser extent due to RUE. Given the delayed phenological development of canaryseed with delayed seeding (Chapter 6), relative to that of wheat and oat, and given that relatively lower amounts of rainfall were available towards the end of the growing season, these increased the potential for water-stressful conditions, especially for canaryseed due to its shallow root system. Reduced HIs in cereals related to water stress and delayed phenological development have been reported for a

series of crops such as spring wheat (Hucl and Baker, 1987), durum wheat (Giunta et al., 1993), triticale (Campuzano et al., 2012), rice (Jearakongman et al, 1995) and maize (Richards, 1996 and references therein). In contrast to canaryseed, wheat and oat, which had higher HIs also had faster development towards anthesis and smaller reductions of HI with late seeding. The delayed phenological development of the pubescent cultivar Keet compared to CDC Bastia likely accounted for differences found between the two cultivars. Keet had larger reductions in HI compared to the two glabrous canaryseed cultivars. A strategy that might be considered for improving canaryseed yield characteristics would be the adjustment of phenological development as it has been implemented in other cereals in order to avoid terminal drought (Araus et al., 2002 and references therein). With regards to the canaryseed biomass production, reductions were mainly through reduced RUE even though $CIPAR_{E\text{-}A}$ also explained the crop biomass, especially with early seeding. The impact of testing environments on RUE was more evident in the post-anthesis phase of the canaryseed crop cycle likely due to increasing frequency of water- and/or heat-stressful conditions, especially with late SDs. The CIPAR, in turn, appeared to have been affected less than the RUE likely due to increased duration of pre-anthesis and crop life cycle with late seeding which however, did not translate into higher biomass and/or grain yield. Results of this study are consistent with results from studies on the growth and biomass components of other temperate cereals, which reported reduced RUE due to water stress in barley (Jamieson et al., 1995b), in wheat and in triticale (Estrada-Campuzano et al., 2012). With regards to the grain yield, the putative importance of the contribution of tiller grain yield to total canaryseed grain yield that was indirectly addressed in earlier studies (Miller, 2000 and May et al., 2012a) is quantitatively supported in the present study. In environments where canaryseed tiller grain yield was substantially reduced, it coincided with whole plant grain yield reduction. Main stem grain yield of canaryseed was relatively more stable. Grain yield of wheat and oat plants depended predominently on main stem grain yield. This is in contrast with other temperate cereals when grown under the long days of high latitudes (Peltonen-Sainio et al., 2009). The grain yield of canaryseed was strongly associated with one of the main determinants, namely the grain number per unit of cultivated area. This is in agreement with previous reports on canaryseed (Bodega et al., 2003; Cogliatti et al., 2011) and other temperate cereals (Peltonen-Sainio et al., 2007). In addition, this agrees with the hypothesis that the grain yield of cereals is related to the capacity of the inflorescence to sink in the photo-assimilates (Boras et al., 2004). However, the photo-assimilate availability during the grain filling period seems also important for reasons related to GLAI, individual leaf area of the upper phytomers, and the duration in Tt from TS to anthesis.

8.2 Future research

Temperate cereal phenological development is primarily determined by temperature, per se, low-temperature vernalization, and photoperiod prior to, as well as, post-vernalization saturation. The impact of temperature on canaryseed phenology was quantified and a putative low-temperature vernalization requirement of canaryseed was observed. The role of photoperiod is less clear, however, and its determination is important in a better understanding canaryseed phenology. The photoperiods used in the present study were ~16 and 20 hours in the field- and the controlled-environment experiments, respectively. As discussed in section 4.4.1., the interaction between the long photoperiod with temperature during vernalization is potentially related to the delayed phenological development of canaryseed observed with delayed seeding, which, in turn, was related to larger yield reductions relative to wheat and oat. It is anticipated that the investigation of the role of photoperiod on canaryseed phenology under a wider range (eg, from 8h to 20h) in factorial combination with more and less vernalization-effective temperatures (eg, 10°C and 15°C) would provide important information relevant to canaryseed phenology. Of interest as well would be the use of cultivars or lines contrasting in phenology to determine whether there is sufficient genetic variation to encourage the breeding of cultivars with the desired level of sensitivity to vernalization and photoperiod. In addition, it would be informative to supplement the time-consuming methodology used in the present study with molecular analysis of plant tissues sampled from material used in the experiments. This would provide additional evidence regarding the vernalization response of canaryseed by more accurately determining the timing of specific developmental events. The difference in the FLN between the two different post-vernalizing plant growth conditions that were previously exposed to short-day (8h) vernalizing conditions (section 4.4.3) suggested that the three-hours-longer photoperiod (ie, from 17h to 20h) increased the FLN of the canaryseed cultivars CDC Bastia and Keet. Canaryseed response to post-vernalizing plant growth conditions is a topic that would require further investigation, together with or separately from the investigation of the role of photoperiod on canaryseed phenology. Once the impact of photoperiod on canaryseed phenology is better understood, experiments with manipulated temperature and photoperiod would assist in quantifying the portion of the yield variability of the crop.

8.3 Overall assessment

Based on evidence provided by the morphological expression of the effect of growing environments that primarily resulted from differences in air temperature, canaryseed has a low-temperature response similar to vernalization requirement. Delayed seeding of canaryseed on

the Canadian Prairies differentially delayed, in terms of Tt, key phenological stages, such as FI, TS formation and anthesis. Despite the shorter phyllochron of canaryseed cultivars to wheat and oat, canaryseed tiller appearance rates were similar, or slightly lower, than those of wheat due to the suppression of the first two or three primary tillers. Canaryseed onset and cessation of tiller appearance shortened the tiller appearance duration, which, together with the suppression of primary tillers, determined the number of tillers that reached physiological maturity. Canaryseed main stem inflorescence growth during stem elongation and grain-filling periods were possibly C-source limited, especially with late SDs. Grain yield was strongly affected by environments where tiller grain yield was reduced. However, main stem grain yield was relatively more stable. In contrast, the grain yield of wheat and oat depended more on main stem yield. Considering all tested environments, canaryseed biomass was similar to that of wheat and lower than oat, along with a lower grain yield relative to both other crop species. Canaryseed grain yield was best explained by changes in HI rather than by changes in biomass. Delayed seeding and delayed phenological development of canaryseed coincided with lower HIs relative to early or optimal seeding date. In contrast, wheat and oat reached anthesis earlier with later SDs and had smaller reductions in HI. The pubescent canaryseed cultivar Keet reached anthesis later, relative to the other canaryseed cultivars and had larger reductions in HI and grain yield with late seeding. The grain yield of canaryseed was strongly associated with the grain number per unit of cultivated area.

Overall, growers are encouraged to choose cultivars with heavier seeds which are likely to show higher early vigor and thus enhanced seedling emergence, early growth, development and crop establishment. Provided the high importance of the timing of agrochemicals, farmers should keep in mind the delayed phenological development of canaryseed cultivars, such as those tested in the present study, with delayed seeding in order to precisely determine the best timing for inputs, fungicides and herbicides application. Given the relatively low individual leaf area of the top few leaves in canaryseed, it may be important for the growers to timely take action, such as the scouting for pests and diseases, in order to retain the good contidion of the leaves preceding the flag leaf. Therefore, it is recommended that for greater grain yield stability, growers should avoid seeding canaryseed cultivars such as those tested in the present study in environments similar to those met with late and very late seeding for a number of reasons related to unfavorable seedbed conditions, potential shortage of soil available moisture delayed phenological development and alterations in phase-duration and the concomitant alterations in photo-assimilate production and distribution.

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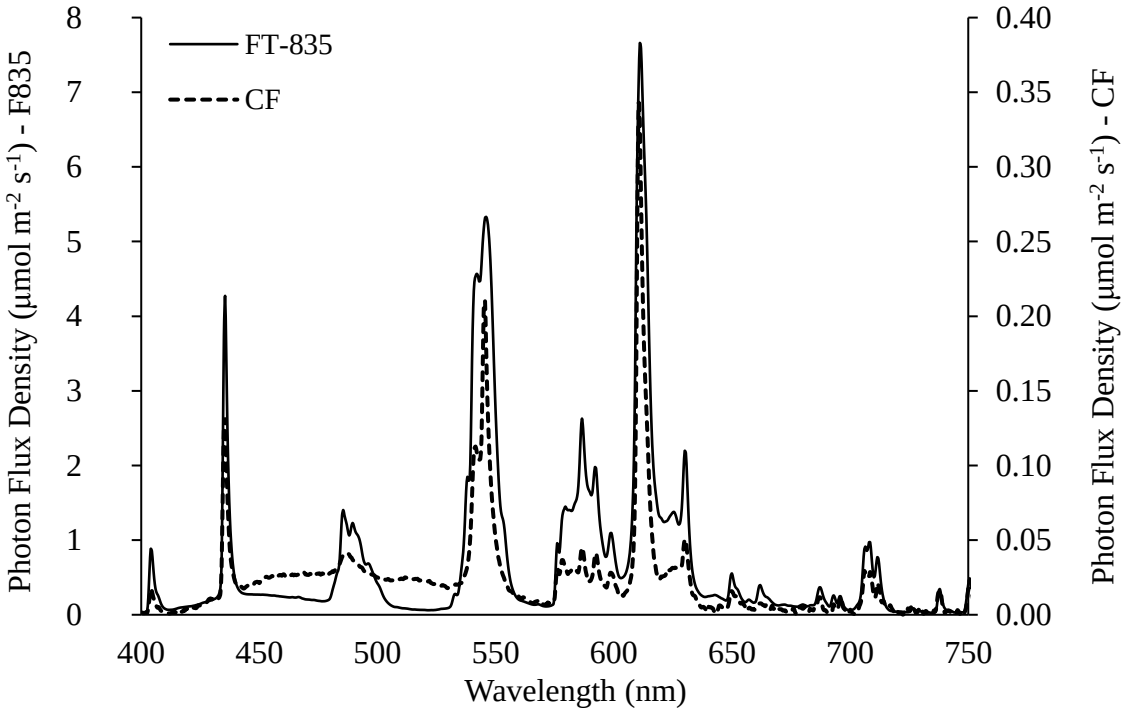
Appendices

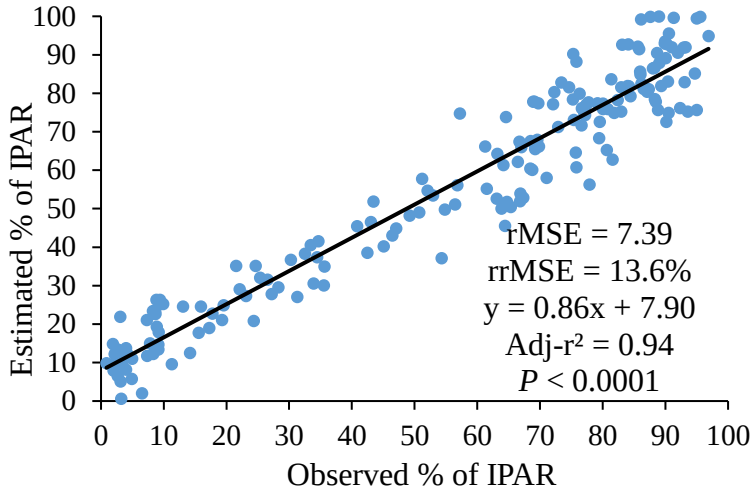
A. 1. Final leaf number for two canaryseed, one wheat and one oat cultivar vernalized at three air temperatures for five durations.

Cultivar	Vernalizing duration (d)					Stat. An.	
						SEM	Sign.
	0	2	7	14	21		
	5°C - 20h photoperiod						
Bastia	-	11.6[a]	10.9[a]	10.9[a]	11.6[a]	0.27	+
Keet	-	17.3[a]	16.6[a]	15.4[a]	16.1[a]	0.60	ns
Barrie	-	8.5[a]	8.2[bc]	8.4[ab]	8.0[c]	0.08	**
Morrison	-	9.1[ab]	9.0[ab]	9.1[a]	8.8[b]	0.10	*
	10°C - 20h photoperiod						
Bastia	11.4[a]	10.3[ab]	10.1[b]	9.1[c]	9.9[bc]	0.27	***
Keet	16.9[a]	16.3[ab]	15.0[b]	13.0[c]	12.9[c]	0.43	***
Barrie	8.4[a]	8.4[a]	8.1[ab]	7.9[b]	7.9[b]	0.11	***
Morrison	9.1[a]	8.7[ab]	8.6[ab]	8.5[b]	8.4[b]	0.15	**
	15°C - 20h photoperiod						
Bastia	-	11.8[a]	11.7[a]	12.0[a]	13.5[a]	0.47	+
Keet	-	18.8[a]	17.1[a]	19.6[a]	17.4[a]	0.81	+
Barrie	-	8.4[a]	8.5[a]	8.4[a]	8.7[a]	0.15	ns
Morrison	-	8.8[a]	8.9[a]	8.9[a]	8.8[a]	0.11	ns

[1]: Means within a cultivar and vernalizing temperature followed by the same superscript letters do not differ significantly at the 5% level. Means separation conducted by Tukey test.



A. 2. Spectral distribution of the photon flux density in one of the growth chambers used in the controlled-environment experiment at 20°C, 535 and 19 µmol m^{-2} s^{-1} obtained by fluorescent tubes (FT-835) and compact fluorescent bulbs (CF), respectively.



A. 3. Observed versus estimated (Beta function) percentage of intercepted PAR. Data points correspond to observational events (average of four individual observations) on two blocks seeding date^{-1} year^{-1} and one or two replications block^{-1} (three or four replications in total). The root mean squared error (rMSE) and the relative root mean squared error (rrMSE) were used as measures of the goodness of fit.

A. 4. Probability values for the folded F-test, the t-test and the data normality test for both seeding dates and each date separately for the modified Haun leaf stage at maximum number of tillers plant^{-1} ($MHLS_{YL}$ at $TilNo_{max}$), thermal time from crop emergence (Tt) at TilNomax prior to flag leaf ligule (FLL) appearance and past that for the canaryseed cultivar CDC Bastia when sown early and late in 2013 and 2014.

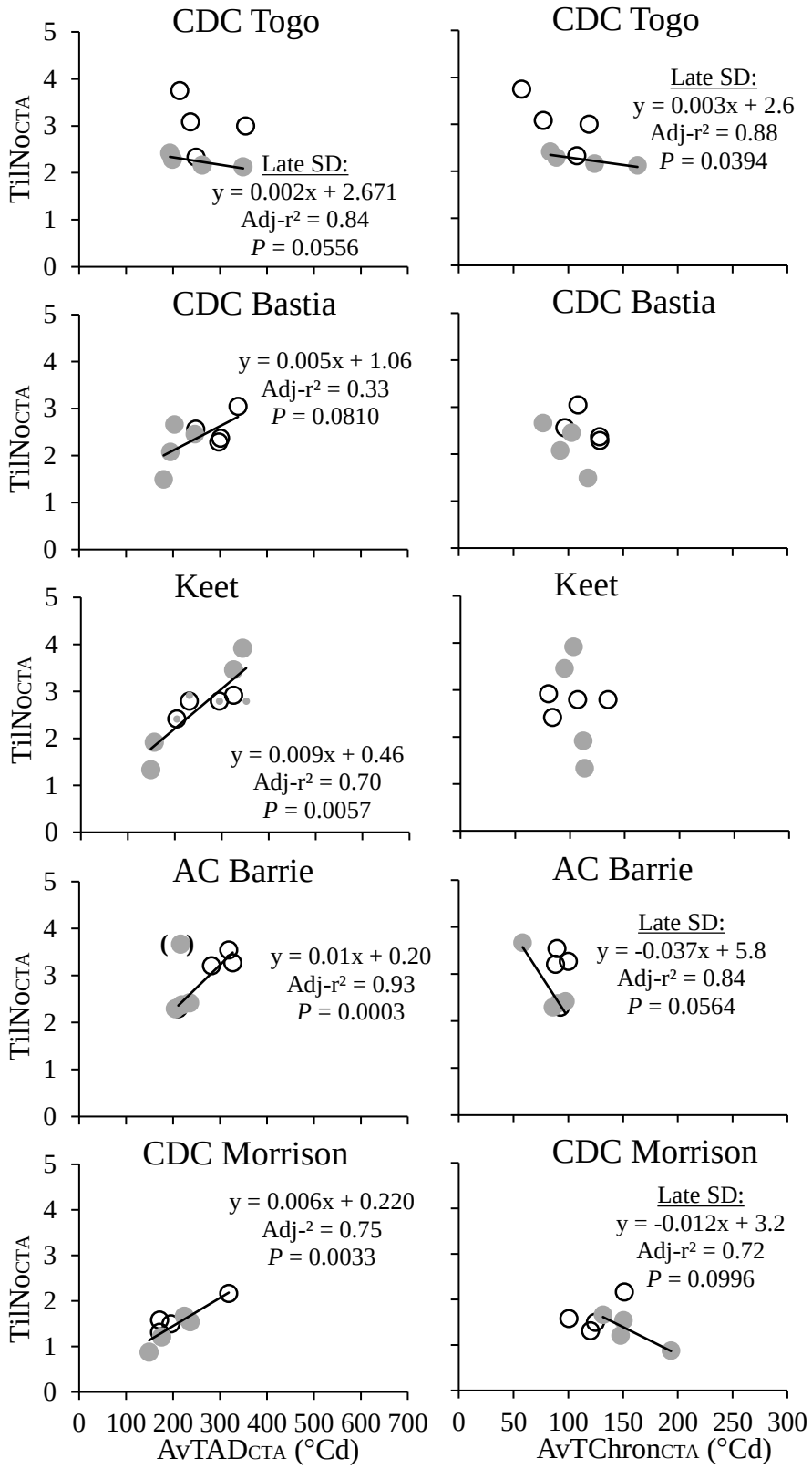
Year	Response variable	*P -value*				
				Test for normality		
		Folded F-test	Pooled t-test	All data	Early	Late
2013	MHLSYL at TilNomax	0.4559	0.0480	0.4873	0.1150	0.9886
2013	Tt at TilNomax prior to FLL	0.4739	0.0343	0.2597	0.012	0.9778
2013	Tt at TilNomax past FLL	0.6836	0.0436	0.9391	0.5805	0.9778
2014	MHLSYL at TilNomax	0.4348	0.2831	0.5755	0.2645	0.6639
2014	Tt at TilNomax prior to FLL	0.7340	0.9333	0.6410	0.6818	0.9375
2014	Tt at TilNomax past FLL	0.3512	0.0001	0.1347	0.6818	0.6547

Tests were conducted between the two seeding dates within each year.

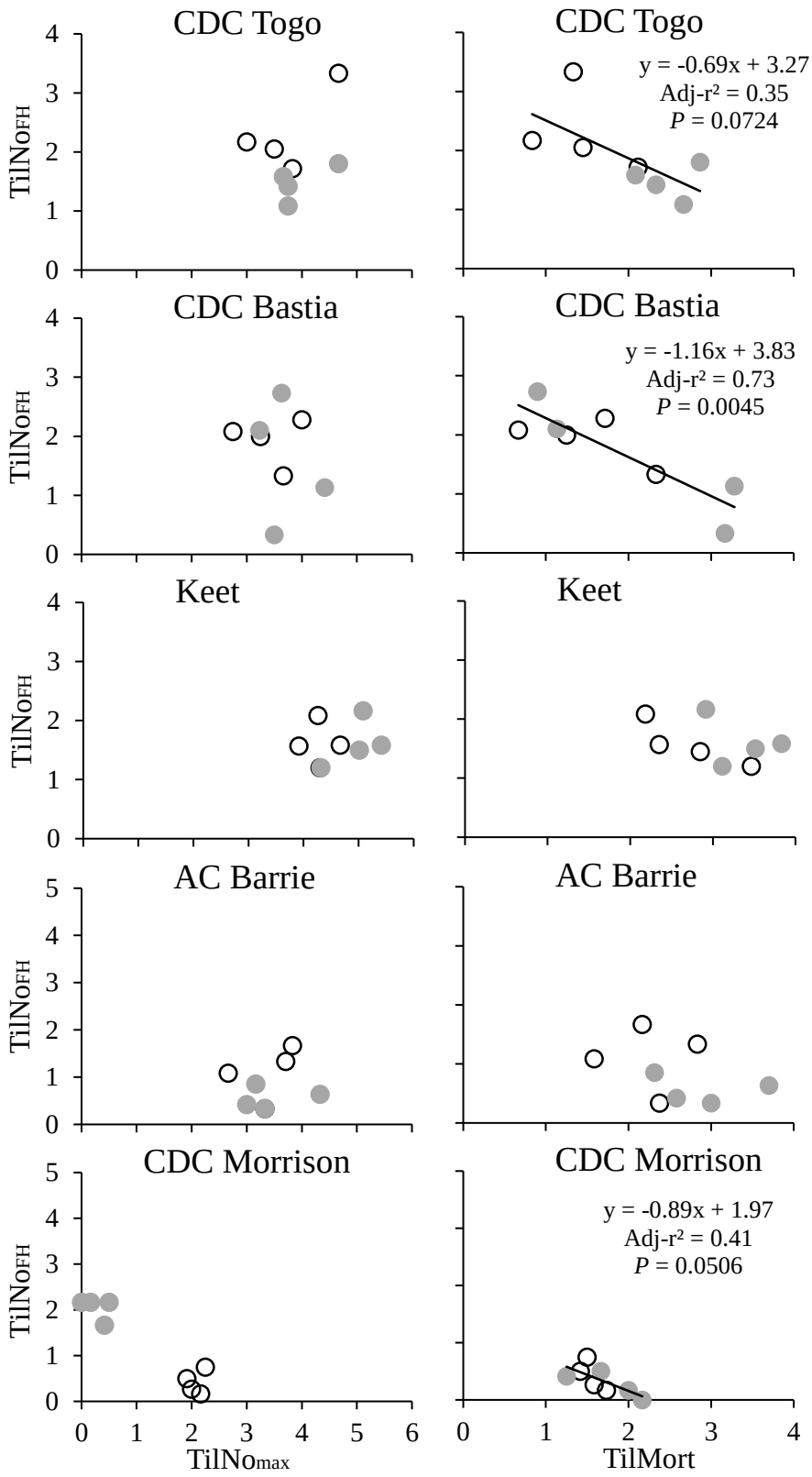
A. 5. Probability values for the folded F-test, the t-test and the data normality test for both seeding dates and each date separately for the percentage of PAR intercepted at maximum number of tillers plant^{-1} (%IPAR at TilNomax) prior to and past the flag leaf ligule (FLL) appearance for the canaryseed cultivar CDC Bastia when sown early and late in 2013 and 2014.

		P-value				
				Test for normality (based on Shapiro-Wilk test)		
Year	Response Variable	Folded F-test	Appropriate t-test	All data	Early	Late
2013	%IPAR at TilNomax prior to FLL	0.0066	0.9407	0.6429	0.7028	1.000
2013	%IPAR at TilNomax past FLL	0.1495	0.7922	0.5789	0.3472	1.000
2014	%IPAR at TilNomax prior to FLL	0.6802	0.0978	0.4322	0.0076	0.8899
2014	%IPAR at TilNomax past FLL	0.4710	0.0115	0.6286	0.0076	0.7301

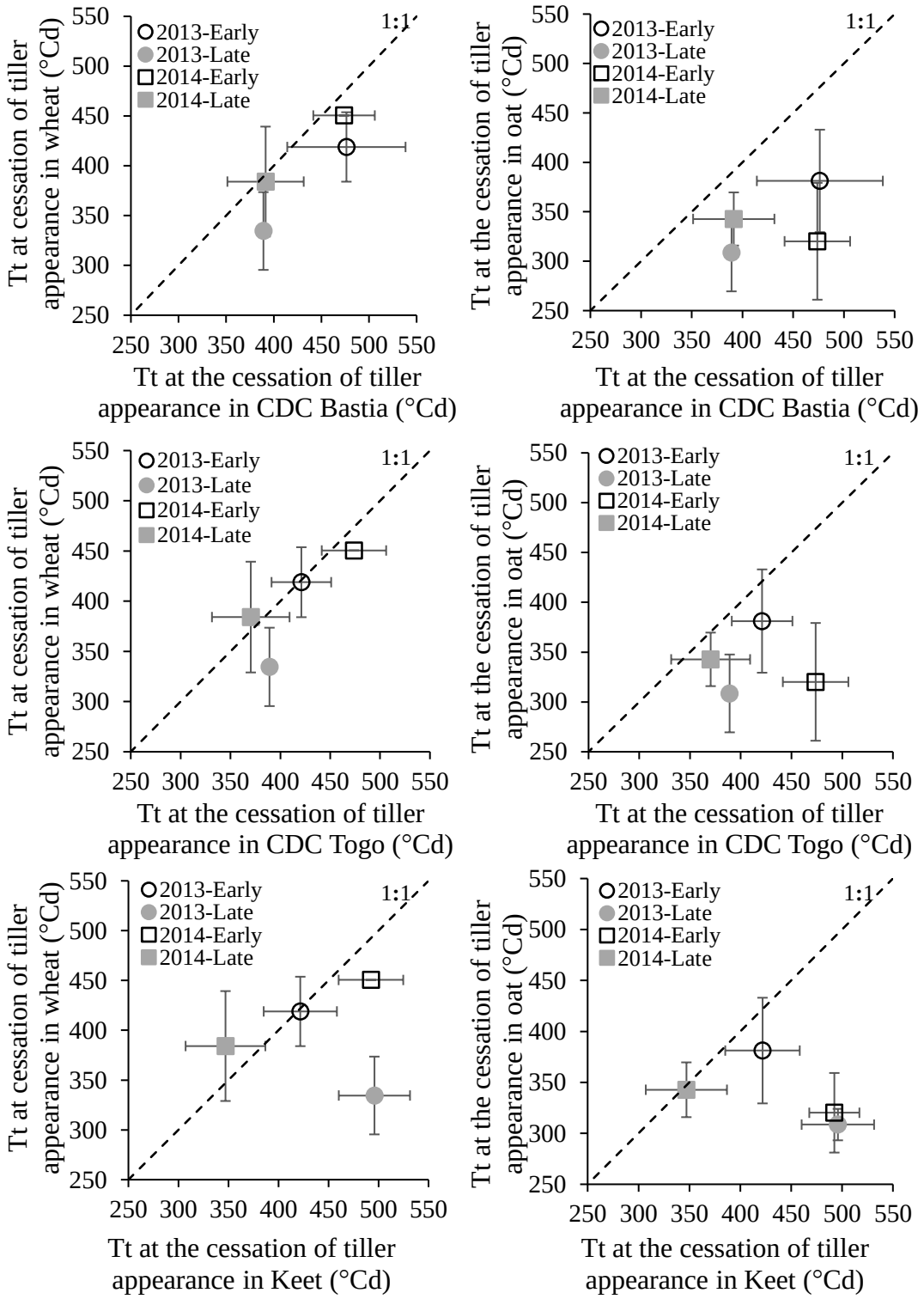
Tests were conducted between the two seeding dates within each year.



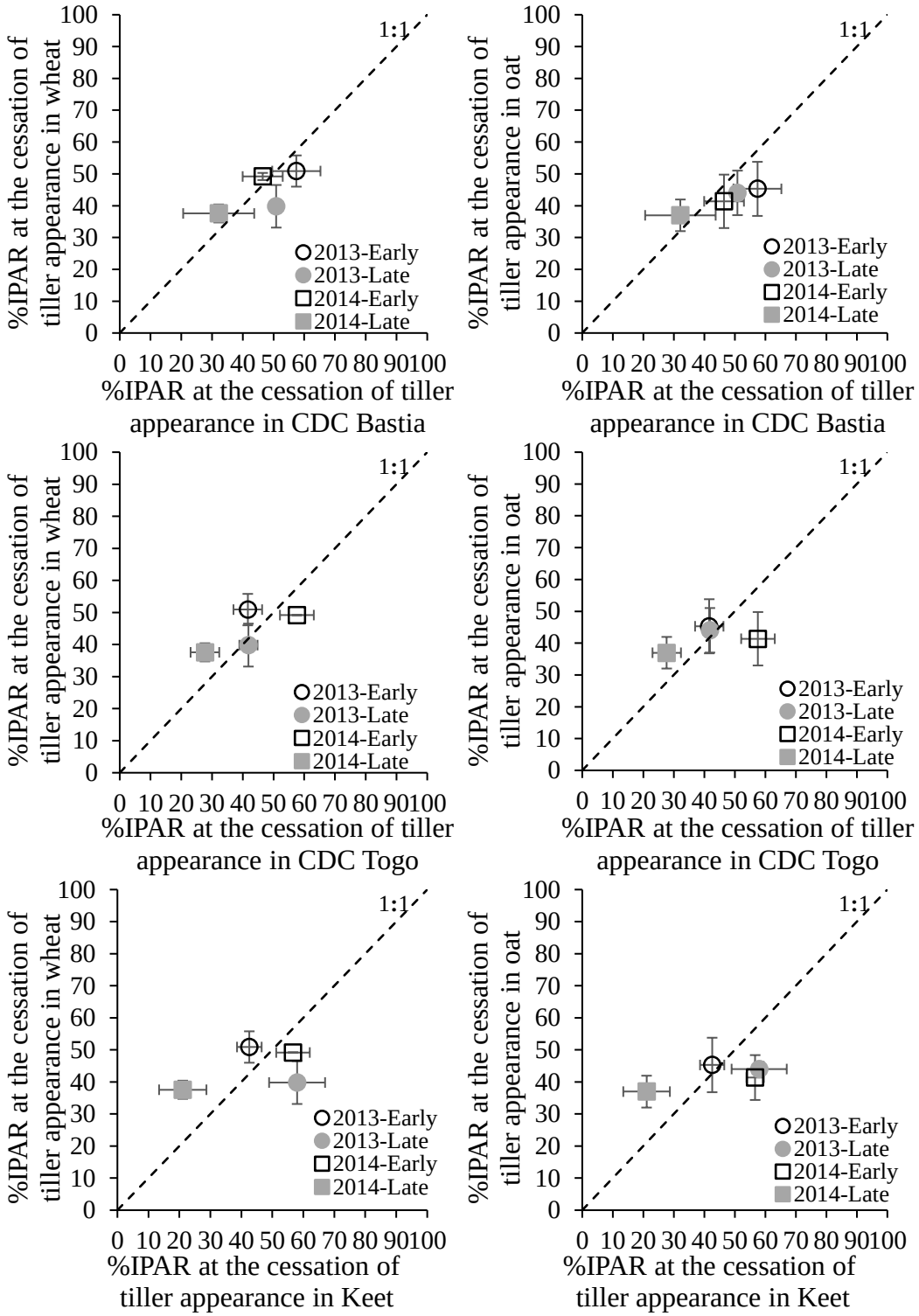
A. 6. Tiller number plant $^{-1}$ (TilNo$_{CTA}$) versus average tiller appearance duration (AvTAD$_{CTA}$) (°Cd) (left) and average thermal time elapsed between consecutive tiller appearance (AvTChron$_{CTA}$) (°Cd) (right) at the cessation of tiller appearance for three canaryseed, one wheat and one oat cultivar seeded early and late in 2013 and 2014. Mean values are derived from observations conducted on two blocks seeding date^{-1}, two replications block^{-1} and six plants replication^{-1}.



A. 7. Tiller number plant $^{-1}$ at final harvest (TilNo$_{FH}$) versus maximum tiller number plant^{-1} (left) and tiller mortality (TilMort = TilMo - TilNoFH) (right) for three canaryseed, one wheat and one oat cultivars sown early, late in 2013 and 2014. Mean values are derived from observations conducted on two blocks seeding date^{-1}, two replications block^{-1} and six plants replication^{-1}.



A. 8. Comparison between canaryseed cultivars and wheat (left) and oat (right) in the thermal time elapsed from emergence (Tt) at the cessation of tiller appearance when seeded early (open symbols) and late (closed grey symbols) in 2013 and 2014. Data points represent means of two blocks, two replications block^{-1} and six plants replication^{-1}.



A. 9. Comparison between canaryseed cultivars and wheat (left) and oat (right) in the percentage of PAR intercepted (%IPAR) at the cessation of tiller appearance when seeded early (open symbols) and late (closed grey symbols) in 2013 and 2014. Data points represent means of two blocks and two replications block^{-1}.

A. 10. Observed and/or estimated modified Haun leaf stage (MHLS) at floral initiation (FI) and terminal spikelet (TS) formation of three canaryseed, one spring wheat and one oat cultivar seeded on three seeding dates in 2013 and 2014.

Cultivar	Stat.An.[1]				Stat. An.					Stat. An.	
					SEM	Sign.				SEM	Sign.
		2013					2014				
		Early	Late	V.Late			Early	Late	V.Late		
		MHLS (or HS for wheat and oat) at FI									
Togo		1.96a[4]	3.08ab	**4.21a**	0.297	*[6]	*2.27*cd[7]	*3.02*bc	***3.69*ab*[5]	0.097	*
Bastia		2.44a	2.69bc	3.67a	0.193	+	2.11d	2.54cd	3.61b	0.196	+
Keet		2.34a	3.52a	**4.11a**	0.140	*	2.43c	3.74a	4.42a	0.260	+
Barrie		2.06a	2.33c	**3.08a**	0.096	*	2.71b	2.31d	2.74a	0.055	+
Morrison		2.81a	**3.09ab**	**3.76a***	0.043	**	3.05a	3.08b	3.45b	0.158	ns
	SEM[2]	0.224	0.083	0.192			0.043	0.079	0.279		
	Sign.[3]	ns	**	+			***	**	+		
		MHLS (or HS for wheat and oat) at TS									
Togo		4.56a	-	7.90a	0.346	+	*4.13*a	*6.09*b	***7.86*a**	0.256	*
Bastia		4.09a	7.11b	7.09ab	0.581	+	3.67a	4.47c	6.92ab	0.409	+
Keet		5.38a	**9.50a**	8.23a	0.383	*	4.89a	**7.68a**	**7.96a**	0.529	*
Barrie		4.05a	4.33c	**5.08c***	0.096	*	4.71a	4.31c	4.73c	0.055	+
Morrison		4.29a	**4.62c**	**5.39bc***	0.046	**	4.57a	4.60c	5.03bc	0.182	ns
	SEM	0.304	0.329	0.408			0.196	0.131	0.523		
	Sign.	ns	**	**			+	***	**		

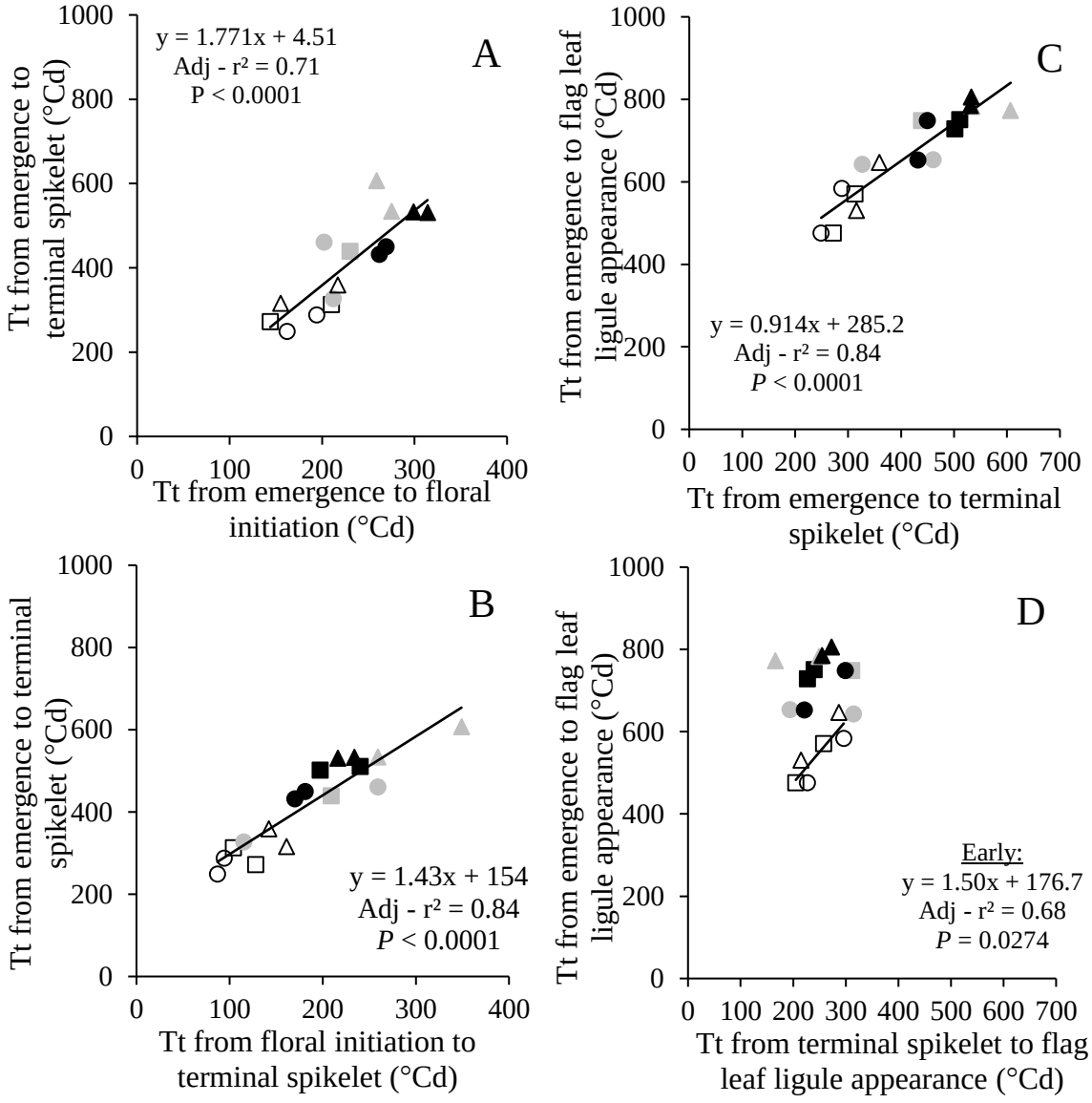
[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance

[4] Cultivar means within a response variable and within a year × seeding date combination followed by the same letters do not differ significantly at 5% level. Mean separations conducted by Tukey's tests.

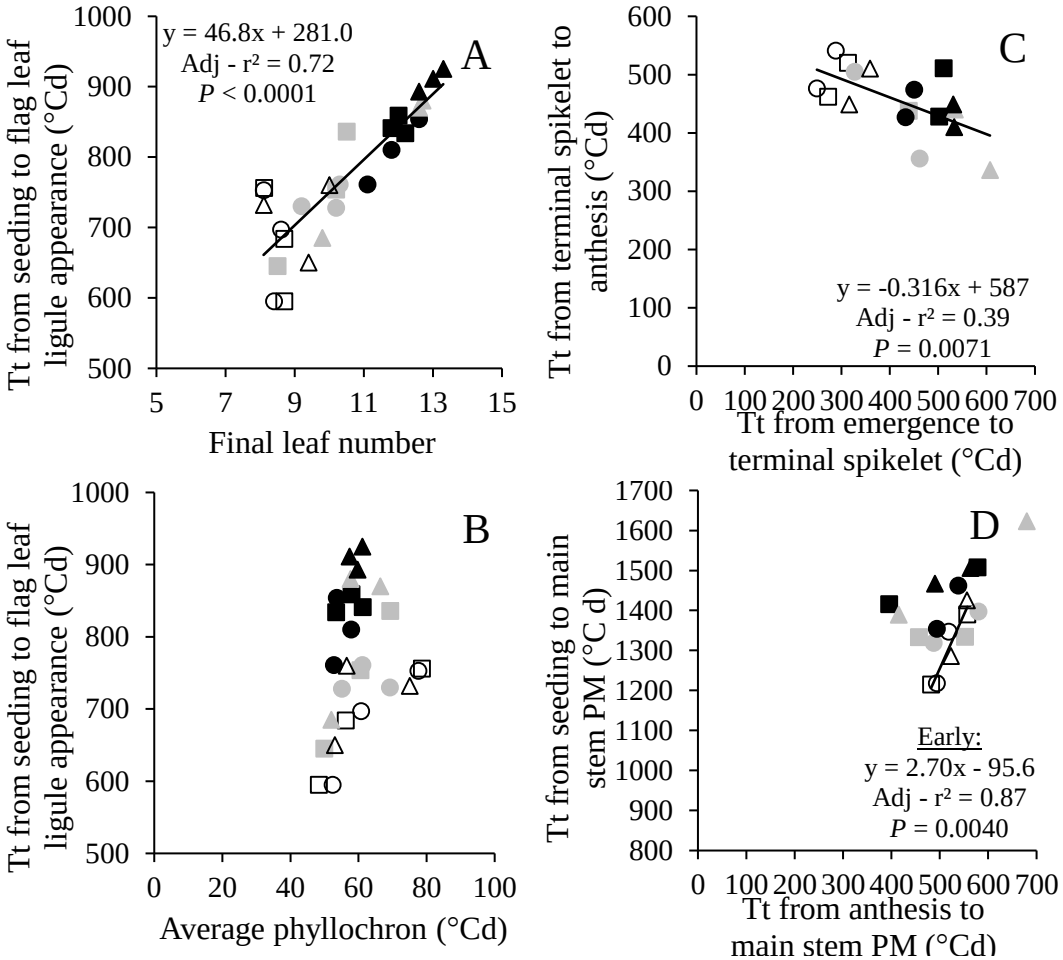
[5] Seeding date means in bold differ significantly from the early seeding date mean within a response variable and within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a response variable and within a year × cultivar combination. Mean separations were conducted by Tukey's tests.

[6] ns, +, *, ** and *** used to denote that the statistical significance within a response variable and within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.

[7] Means in italic are estimates obtained from model functions developed for the cultivar CDC Bastia as described in Section 6.2.4.1. and presented in the Appendices 13 and 14.



A. 11. Thermal time (Tt) elapsed from emergence to terminal spikelet versus the Tt from emergence to floral initiation (A); Tt elapsed from emergence to terminal spikelet versus the Tt from floral initiation to terminal spikelet (B); Tt elapsed from emergence to flag leaf ligule appearance versus the Tt elapsed from emergence to terminal spikelet (C); and Tt elapsed from emergence to flag leaf ligule appearance versus the Tt elapsed from terminal spikelet to flag leaf ligule appearance (D) for the canaryseed cultivars CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) seeded early (empty symbols), late (grey-closed symbols) and very late (black-closed symbols) in 2013 and 2014.



A. 12. Thermal time (Tt) elapsed from seeding to flag leaf ligule appearance versus the final leaf number on main stem (A) and versus the average phyllochron (B); Tt elapsed from terminal spikelet to anthesis versus the Tt elapsed from emergence to terminal spikelet (C) and Tt elapsed from seeding to main stem physiological maturity versus the Tt elapsed from anthesis to main stem physiological maturity (D) for the canaryseed cultivars CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) seeded early (empty symbols), late (grey-closed symbols) and very late (black-closed symbols) in 2012, 2013 and 2014 (panels A and B) and only in 2013 and 2014 (panels C and D).

A. 13. Parameters, measures of goodness of fit and significance of the simple linear regression models between the final leaf number (FLN) and the modified Haun leaf stage (MHLS) at floral initiation (FI) and at terminal spikelet formation (TS) for the canaryseed cultivars CDC Bastia and Keet.

Phenological stage	CDC Bastia					Keet				
	Model parameters		Measures of goodness of fit		Significance	Model parameters		Measures of goodness of fit		Significance
	a[1]	b[2]	rMSE	Adj-r²	*P*-value	a	b	rMSE	Adj-r²	*P*-value
FI	4.20	2.01	0.484	0.88	0.0039	6.20	1.50	0.334	0.94	0.0010
TS	5.62	0.77	0.574	0.82	0.0078	6.64	0.65	0.745	0.69	0.0261

[1]: intercept; [2]: slope

Note 1: The regression analyses were done on the means obtained from two years and three seeding dates year^{-1}. Each mean was derived from two blocks seeding date^{-1} and three or four replications block^{-1} (n=6).

Note 2: Comparison of the two cultivars regression lines for MHLS at FI according to Fisher (1921) indicated that regression slopes are statistically different. Therefore, the observations from these two cultivars could not be pooled and different regression parameters were required for the determination of the MHLS at FI for different canaryseed cultivars.

A. 14. Observed and predicted modified Haun leaf stage (MHLS) at floral initiation (FI) and terminal spikelet (TS) formation for the canaryseed cultivar CDC Togo when seeded on three dates in 2013.

Seeding Date						rMSE[3]	
Early		Late		V. Late		B.	K.
Observed MHLS$_{FI}$							
1.96		3.08		4.21			
Observed MHLS$_{TS}$							
4.56		-		7.90			
Predicted MHLS$_{FI}$							
B.[1]	K.[2]	B.	K.	B.	K.		
2.24	1.67	2.98	2.67	3.98	4.01		
Predicted MHLS$_{TS}$							
B.	K.	B.	K.	B.	K.		
4.01	3.20	-	-	8.57	8.62		
Observed-Predicted MHLS$_{FI}$							
B.	K.	B.	K.	B.	K.		
-0.28	0.29	0.10	0.41	0.23	0.20	0.48	0.33
Observed-Predicted MHLS$_{TS}$							
B.	K.	B.	K.	B.	K.		
0.55	1.36	-	-	-0.67	-0.72	0.57	0.75

[1] : Model function based on observations on the cultivar CDC Bastia
[2] : Model function based on observations on the cultivar Keet
[3] : rMSE stand for root mean square error and is used as a measure of the goodness of fit

A. 15. Main stem and tillers inflorescence dry weights at final harvest for three canaryseed, one spring wheat and one oat cultivar seeded on three seeding dates in 2012.

Cultivar	Stat. An.[1]				Stat. An.	
					SEM	Sign.
		Early	Late	V.Late		
	Main stem inflorescence dry weight					
Togo		0.48c[4]	0.48c	0.59b	0.035	+[6]
Bastia		0.54c	0.52c	0.64b*****	0.042	*
Keet		0.73b	0.68b	**0.50b*[5],**	0.046	**
Barrie		1.06a	0.97a	1.05a	0.043	ns
Morrison		-	-	-	-	-
	SEM[2]	0.051	0.052	0.036		
	Sign[3]	***	***	***		
	Tiller inflorescences dry weight					
Togo		1.72a	1.96a	1.45ab	0.206	ns
Bastia		1.76a	2.41a	1.44ab*****	0.449	+
Keet		2.67a	3.09a	**0.96b***	0.637	***
Barrie		2.32a	2.76a	1.93a	0.600	ns
Morrison		-	-	-	-	-
	SEM	2.316	0.611	0.164		
	Sign	+	ns	***		

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance
[4] Cultivar means within a response variable and within a year × seeding date combination followed by the same letters do not differ significantly at 5% level. Mean separations conducted by Tukey's tests.
[5] Seeding date means in bold differ significantly from the early seeding date mean within a response variable and within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a response variable and within a year × cultivar combination. Mean separations were conducted by Tukey's tests.
[6]ns, +, *, ** and *** used to denote that the statistical significance within a response variable and within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.

A. 16. Tiller biomass at terminal spikelet (TS), anthesis (An), post-anthesis (PAn) and final harvest (FH) for three canaryseed, one spring wheat and one oat cultivar seeded early and late in 2013 and 2014.

Cultivar	Stat.An.[1]	2013		Sign.	2014		Sign.
		Early	Late		Early	Late	
				Tiller biomass at TS			
Togo		0.01	0.28	**	0.01	0.18	***
Bastia		0.03	0.17	*	0.01	0.03	***
Keet		0.02	0.67	*	0.00	0.22	***
Barrie		0.06	0.13	**	0.02	0.10	***
Morrison		0.06	0.10	+	0.03	0.04	ns
	SEM	0.006	0.108		0.004	0.022	
	Sign.	**	**		***	***	
				Tiller biomass at An			
Togo		1.67	5.39	***	1.95	1.63	ns
Bastia		1.48	4.65	**	1.69	1.00	*
Keet		2.42	4.83	*	2.14	2.14	ns
Barrie		1.42	3.95	***	2.10	1.57	ns
Morrison		0.60	3.43	***	0.06	0.36	**
	SEM	0.207	0.563		0.384	0.225	
	Sign.	***	+		**	***	
				Tiller biomass at PAn			
Togo		2.54	2.03	ns	3.06	3.34	ns
Bastia		1.89	1.09	ns	2.74	1.94	ns
Keet		3.41	1.80	+	3.03	2.41	ns
Barrie		1.26	1.39	ns	2.36	1.18	*
Morrison		1.25	1.00	ns	0.76	0.77	ns
	SEM	0.444	0.310		0.506	0.468	
	Sign.	**	+		*	**	
				Tiller biomass at FH			
Togo		3.91	1.66	**	2.72	1.77	*
Bastia		2.40	0.45	**	2.88	1.71	ns
Keet		2.19	1.89	ns	1.96	1.78	ns
Barrie		1.99	0.52	*	1.68	1.08	ns
Morrison		0.90	0.22	*	0.29	0.94	**
	SEM	0.492	0.237		0.405	0.363	
	Sign.	***	***		**	*	
		F-probability and SEM for phenological stage means separation within each year × SD combination					
Togo	SEM	0.325	0.229		0.321	0.346	
	Sign.	**	***		***	*	
Bastia	SEM	0.331	0.435		0.516	0.260	
	Sign.	***	***		**	***	
Keet	SEM	0.402	0.449		0.417	0.355	
	Sign.	***	***		**	**	
Barrie	SEM	0.132	0.182		0.070	0.074	
	Sign.	***	***		***	***	
Morrison	SEM	0.471	0.355		0.306	0.354	
	Sign.	***	***		***	***	

[1]For symbols and abbreviations see A. 15.

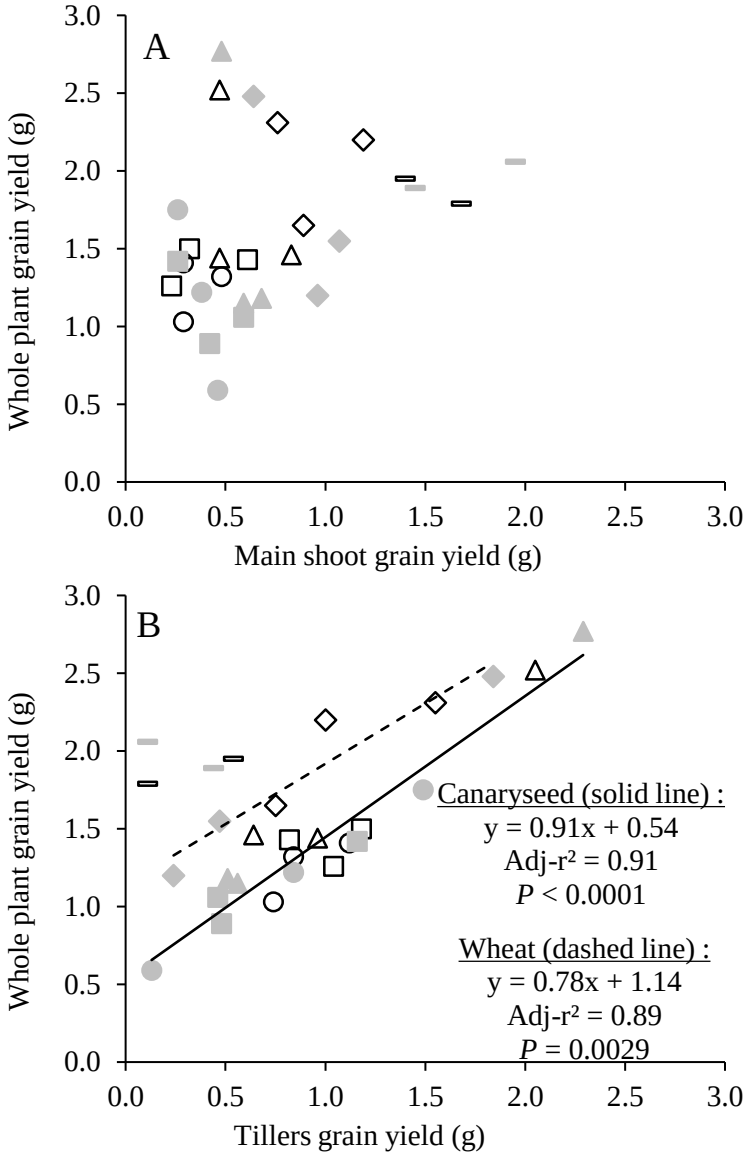
Mean values and separation are based on two blocks per year × seeding date ×cultivar combination, two replications block^{-1} and six plants replication^{-1}.

A. 17. Main stem and tiller grain yield for three canaryseed, one spring wheat and one oat cultivar seeded on two dates in 2012, 2013 and 2014.

Cultivar	Stat. An.[1]	2012		Sign.	2013		Sign.	2014		Sign.
		Early	Late		Early	Late		Early	Late	
					Main stem grain yield (g)					
Togo		0.23(0.021)c[4]	0.26(0.033)c	ns[5]	0.32(0.030)d	0.59(0.055)c	**	0.61(0.029)d	0.42(0.021)d	**
Bastia		0.29(0.046)c	0.26(0.030)c	ns	0.29(0.028)d	0.46(0.013)c	**	0.48(0.021)d	0.38(0.010)d	**
Keet		0.47(0.055)b	0.48(0.042)b	ns	0.47(0.041)c	0.59(0.033)c	+	0.83(0.029)c	0.68(0.042)c	*
Barrie		0.76(0.029)a	0.64(0.027)a	**	0.89(0.030)b	0.96(0.020)b	ns	1.19(0.055)b	1.07(0.106)b	ns
Morrison		-	-	-	1.40(0.037)a	1.95(0.103)a	**	1.68(0.084)a	1.45(0.018)a	*
	SEM[2]	0.061	0.039		0.040	0.067		0.061	0.054	
	Sign.[3]	***	***		***	***		***	***	
					Tiller shoots grain yield (g)					
Togo		1.04(0.105)b	1.16(0.146)	nsb	1.18(0.137)a	0.46(0.058)ab	**	0.82(0.041)ab	0.48(0.070)a	**
Bastia		1.12(0.198)b	1.49(0.274)	nsab	0.74(0.079)ab	0.13(0.037)c	**	0.84(0.080)ab	0.84(0.062)a	ns
Keet		2.05(0.311)a	2.29(0.412)	nsa	0.96(0.216)ab	0.56(0.117)a	ns	0.64(0.208)ab	0.51(0.126)a	ns
Barrie		1.55(0.303)ab	1.84(0.228)	nsab	0.75(0.206)ab	0.24(0.027)bc	*	1.00(0.269)a	0.47(0.225)a	ns
Morrison		-	-	-	0.54(0.153)b	0.11(0.064)c	*	0.11(0.063)b	0.44(0.037)a	**
	SEM	0.441	0.461		0.213	0.073		0.170	0.121	
	Sign.	**	*		*	***		*	+	
					Whole plant grain yield (g)					
Togo		1.26(0.098)b	1.42(0.177)c	ns	1.50(0.119)ab	1.06(0.074)b	*	1.43(0.067)a	0.89(0.090)c	**
Bastia		1.41(0.239)b	1.75(0.282)bc	ns	1.03(0.074)b	0.59(0.043)c	**	1.32(0.059)a	1.22(0.053)bc	ns
Keet		2.52(0.358)a	2.77(0.453)a	ns	1.44(0.245)ab	1.15(0.086)b	ns	1.46(0.214)a	1.18(0.166)bc	ns
Barrie		2.31(0.320)a	2.48(0.226)ab	ns	1.65(0.232)ab	1.20(0.034)b	ns	2.20(0.311)a	1.55(0.175)ab	ns
Morrison		-	-	-	1.95(0.116)a	2.06(0.143)a	ns	1.79(0.146)a	1.89(0.050)a	ns
	SEM	0.496	0.492		0.207	0.099		0.198	0.134	
	Sign.	***	**		**	***		+	***	

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [4] Cultivar means within a response variable and within a year × seeding date combination followed by the same letters do not differ significantly at 5% level. Mean separations conducted by Tukey's tests.

[5]ns, +, *, ** and *** used to denote that the statistical significance within a response variable and within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.



A. 18. Whole plant grain yield versus the main stem grain yield (A) and the tillers grain yield (B) for the canaryseed cultivars CDC Bastia (circles), CDC Togo (squares) and Keet (triangles), for the spring wheat cultivar AC Barrie (diamonds) and for the oat cultivar CDC Morrison (dashes) when seeded early (empty symbols and/or black border) and late (closed symbols and/or grey border) in 2012, 2013 and 2014, except from the oat cultivar for which data are presented for the last two years only.

A. 19. Beta function estimates of maximum crop growth rate (C_m), the time at which C_m was attained (T_m) and the time at which the maximum crop dry weight was reached (Te) and crop growth ceased for three canaryseed, one spring wheat and one oat cultivar seeded on three seeding dates in 2013 and 2014.

Cultivar	Stat.An.[1]				Stat. An. SEM Sign.					Stat. An. SEM Sign.	
		2013					2014				
		Early	Late	V.Late			Early	Late	V.Late		
		Tm (day)									
Togo		62.0ab[4]	59.8a	58.9a	1.12	ns[6]	70.0ab	**61.5bc**	**64.2ab**[5]	1.18	**
Bastia		60.3bc	58.9ab	60.3a	0.71	ns	71.5a	**62.0b**	**61.7b**	1.04	***
Keet		63.3a	63.5a	60.4a	1.21	ns	73.1a	**65.3a**	**67.6a**	0.97	**
Barrie		58.4c	**53.4c**	**50.7b***	0.69	***	68.5ab	**57.4d**	**57.2c**	0.82	***
Morrison		59.0c	**54.5bc**	**49.4b***	0.58	***	66.3b	**58.3cd**	**54.3c***	0.59	***
	SEM[2]	0.97	1.09	0.78			1.16	0.72	0.81		
	Sign.[3]	***[3]	***	***			**	***	***		
		Te (day)									
Togo		79.4a	78.0b	81.6ab	1.54	ns	88.3a	79.7ab	94.0a*	3.17	*
Bastia		78.1a	80.2ab	78.0b	2.14	ns	87.9a	**79.0ab**	85.6ab	1.89	*
Keet		82.0a	84.9a	85.7a	1.14	ns	89.8a	82.8a	93.2a*	2.08	*
Barrie		76.8a	76.1b	**70.4c***	1.75	**	87.8a	**72.2b**	**81.4b***	1.24	***
Morrison		77.3a	76.1b	**69.8c***	1.30	**	86.4a	**75.9ab**	81.8b*	1.38	**
	SEM	1.54	1.67	1.44			1.36	2.20	2.03		
	Sign.	+	**	***			ns	*	**		
		Cm (g m^{-2} d^{-1})									
Togo		24.2a	22.9a	18.0ab	2.07	ns	27.7a	25.1a	17.7b	3.21	ns
Bastia		23.6a	20.1a	23.6a	2.40	ns	32.2a	25.8a	20.5ab	5.40	ns
Keet		24.0a	20.6a	15.8b*	1.96	+	31.3a	27.5a	**18.1b***	1.75	**
Barrie		23.7a	20.6a	23.2a	0.86	+	28.1a	27.3a	22.5ab	3.22	ns
Morrison		27.4a	28.2a	24.9a	2.70	ns	33.3a	28.6a	24.8a	2.92	ns
	SEM	2.24	2.01	2.03			3.55	3.67	1.18		
	Sign.	ns	+	**			ns	ns	**		

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance

[4] Cultivar means within a response variable and within a year × seeding date combination followed by the same letters do not differ significantly at 5% level. Mean separations conducted by Tukey's tests.

[5] Seeding date means in bold differ significantly from the early seeding date mean within a response variable and within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a response variable and within a year × cultivar combination. Mean separations were conducted by Tukey's tests.

[6] ns, +, *, ** and *** used to denote that the statistical significance within a response variable and within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.

A. 20. Estimated maximum relative growth rate (RGR_{max}) and average crop growth rate (CGR) for three canaryseed, one spring wheat and one oat cultivar seeded on three dates in 2013 and 2014.

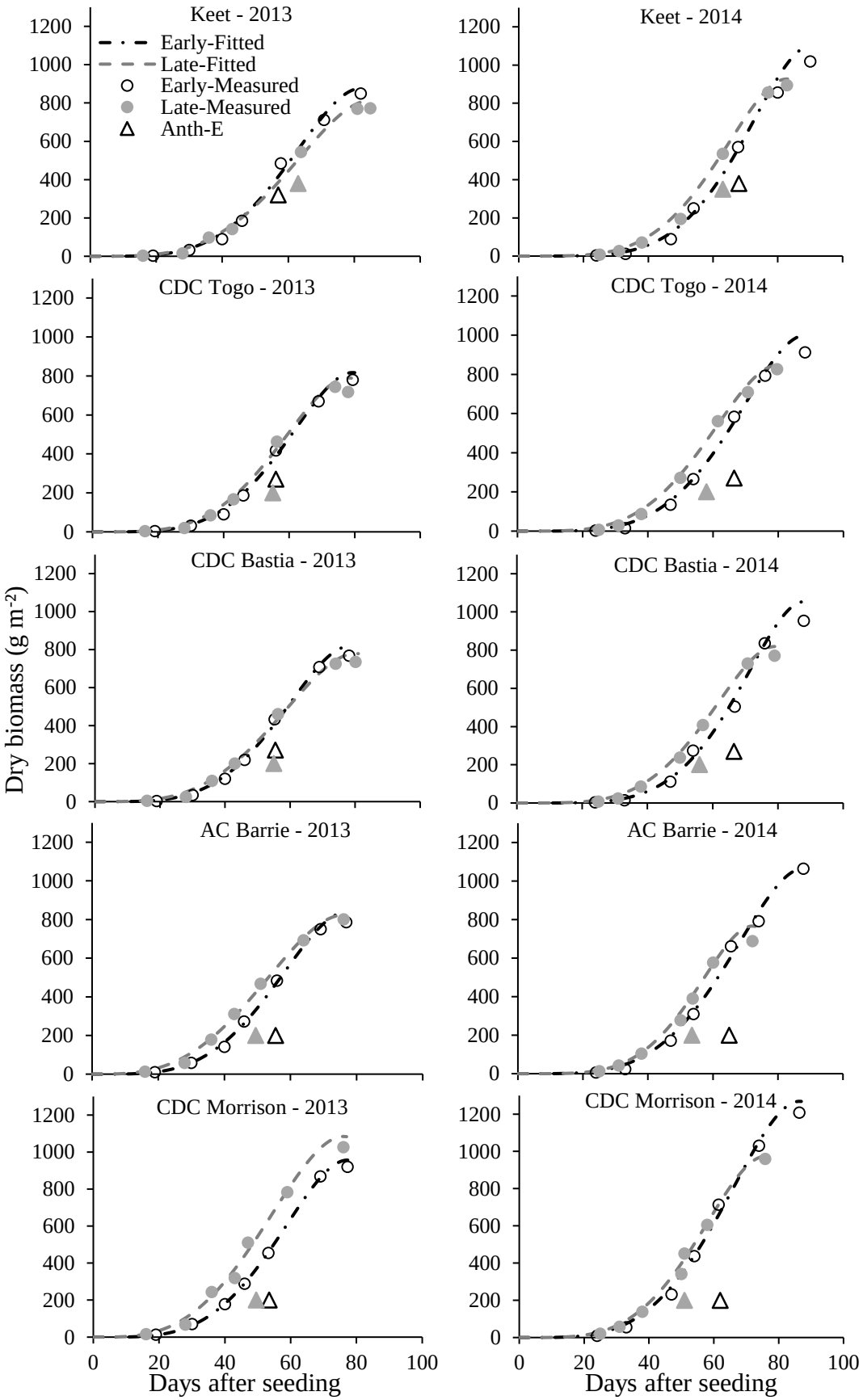
Cultivar	Stat.An.[1]				Stat. An. SEM	Sign.				Stat. An. SEM	Sign.
		2013					2014				
		Early	Late	V.Late			Early	Late	V.Late		
		RGR_{max} ($g\ g^{-1}\ d^{-1}$)									
Togo		0.258b[4]	0.250a	**0.268a*[5]**	0.0065	ns[6]	0.284a	0.294a	0.200ab	0.0066	***
Bastia		0.286a	0.258a	0.286a	0.0086	ns	0.272a	0.287a	0.232a****	0.0116	*
Keet		0.258b	**0.228b**	0.265a****	0.0057	**	0.272a	0.252ab	**0.198ab****	0.0084	***
Barrie		0.212c	0.200c	0.217b****	0.0045	*	0.242b	0.255ab	**0.180b****	0.0079	***
Morrison		0.199c	0.197c	0.210b	0.0041	ns	0.235b	0.227b	**0.201ab****	0.0064	*
	SEM[2]	0.0044	0.0077	0.0068			0.0055	0.0097	0.0113		
	Sign.[3]	***[3]	***	***			***	**	**		
		CGR ($g\ m^{-2}\ d^{-1}$)									
Togo		20.4a	17.9b	15.6bc	1.28	+	23.1a	19.7a	**15.0c**	1.72	*
Bastia		20.6a	16.6b	17.7abc	1.41	ns	24.0a	20.1a	**16.9bc**	2.02	*
Keet		20.8a	15.7b	**13.3c**	1.47	*	23.3a	20.5a	**14.6c****	1.40	**
Barrie		20.9a	18.4ab	20.7ab	0.79	+	24.0a	20.9a	20.8ab	1.79	ns
Morrison		24.0a	24.5a	22.8a	2.36	ns	30.0a	23.1a	24.1a	2.64	ns
	SEM	1.72	1.44	1.49			2.36	2.02	1.18		
	Sign.	ns	**	***			ns	ns	***		

[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance

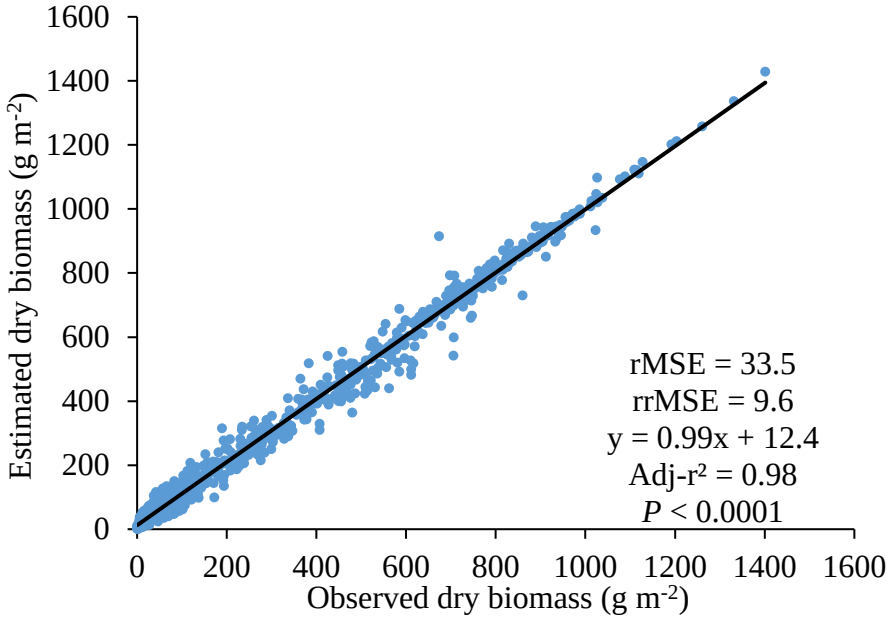
[4] Cultivar means within a response variable and within a year × seeding date combination followed by the same letters do not differ significantly at 5% level. Mean separations conducted by Tukey's tests.

[5] Seeding date means in bold differ significantly from the early seeding date mean within a response variable and within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a response variable and within a year × cultivar combination. Mean separations were conducted by Tukey's tests.

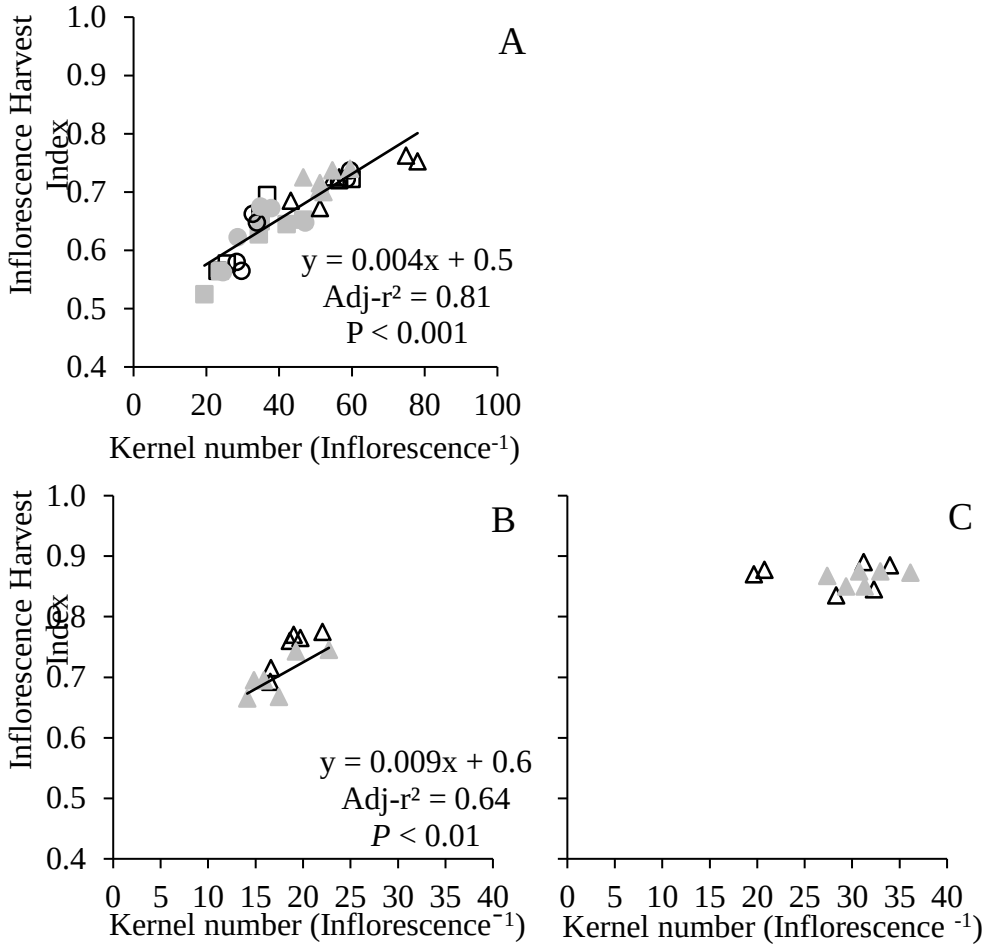
[6] ns, +, *, ** and *** used to denote that the statistical significance within a response variable and within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001.



A. 21. Measured (circle) and fitted (curve) crop biomass for canaryseed, spring wheat and oat cultivars seeded early (black) and late (grey) in 2013 and 2014. Arrows indicate main stem anthesis.



A. 22. Observed versus Beta function predicted dry biomass values for five cultivars seeded on three seeding dates in 2013 and 2014. The root mean squared error (RMSE) and relative mean square error were used as measures of the goodness of fit.



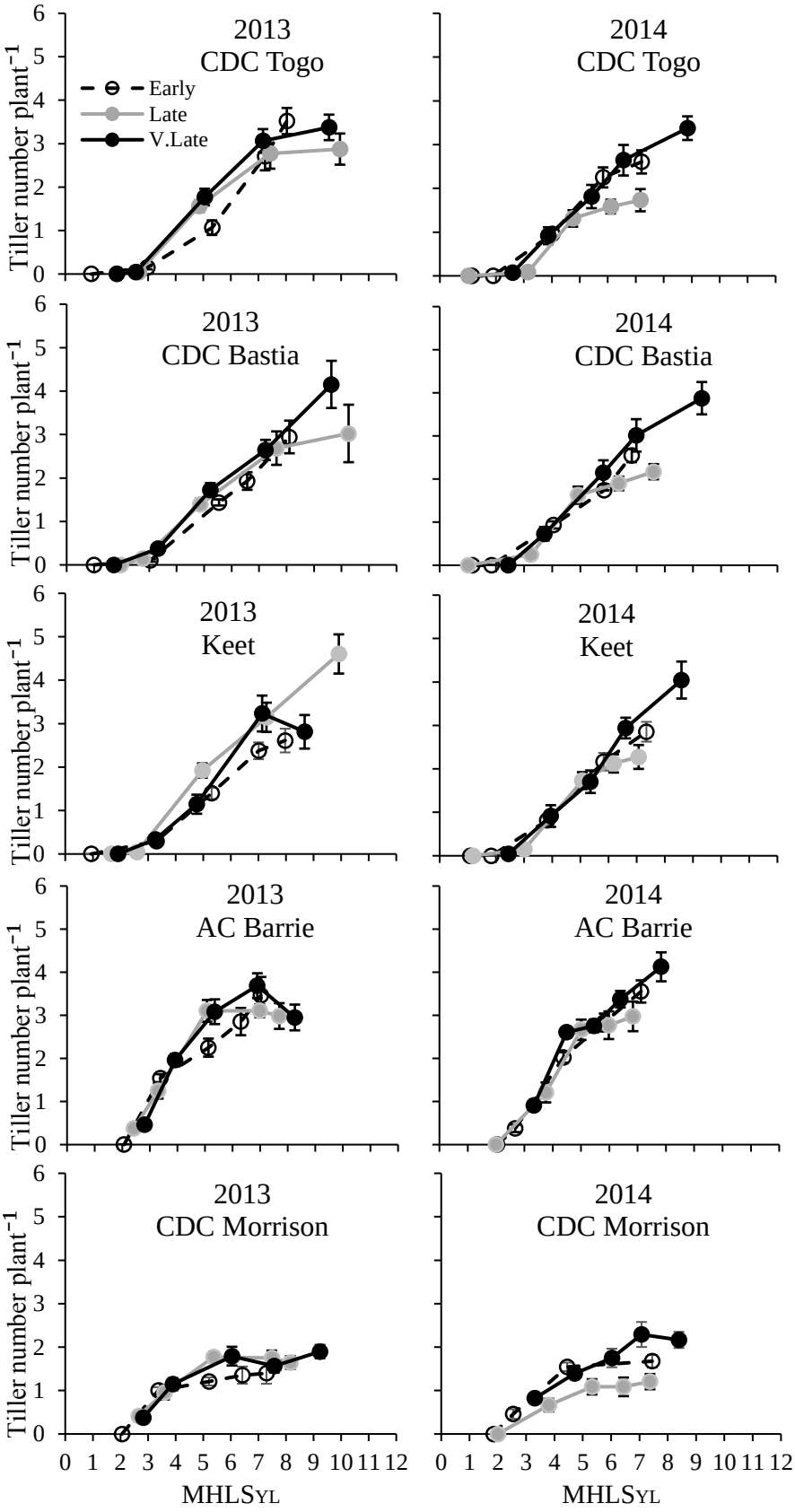
A. 23. Inflorescence harvest index versus the kernel number inflorescence^{-1} for the canaryseed cultivars CDC Bastia (circles), CDC Togo (squares) and Keet (triangles) (A) for the wheat cultivar (B) and for the oat cultivar (C) when seeded early (empty symbols) and late (closed symbols) in 2013 and 2014.

Results with all 3 SDs and all 4 replications/block

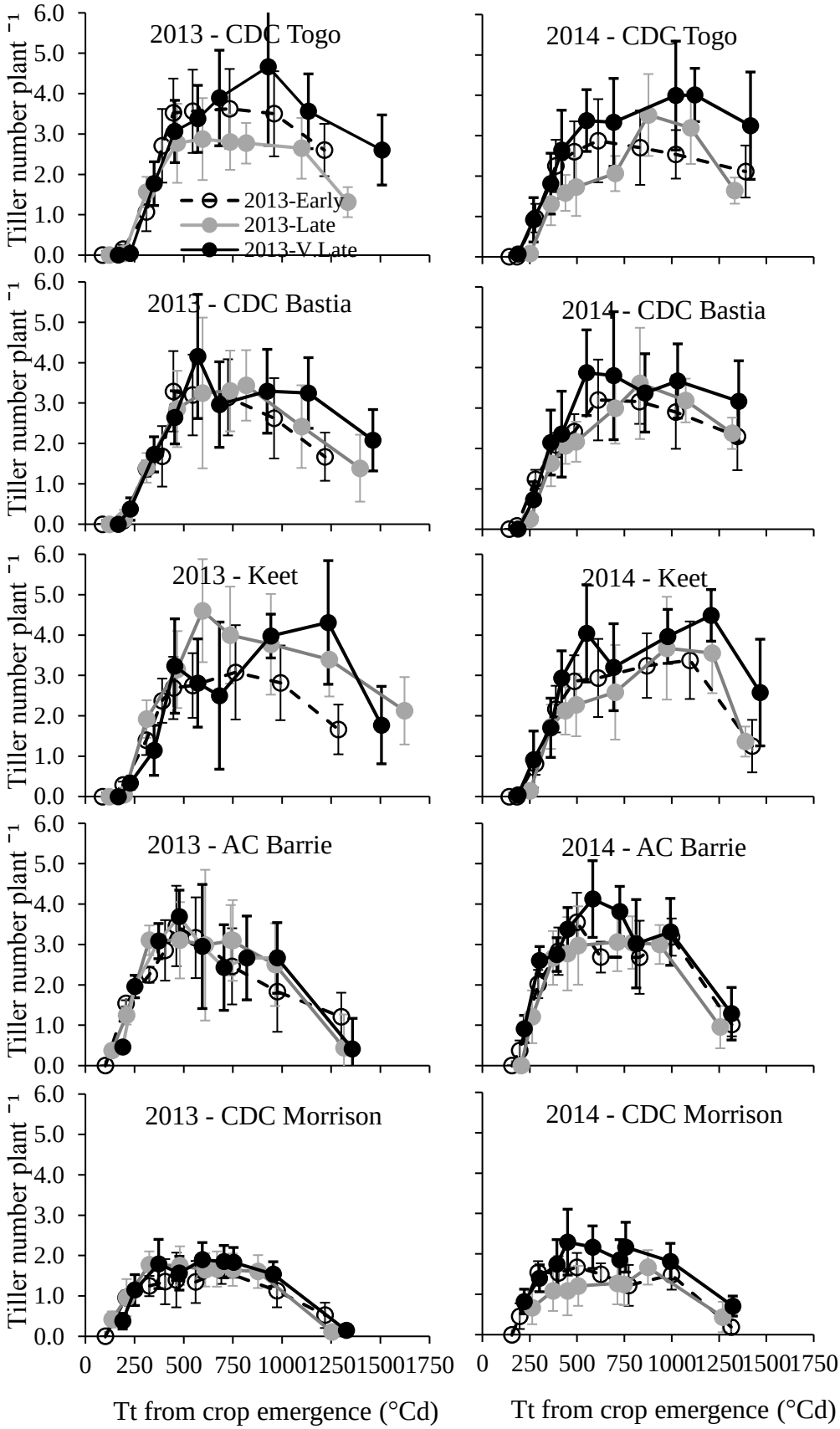
A. 24. Elapsed thermal time after crop emergence (Em) (Tt) to the onset of tiller appearance, Beta function estimates of Tt at the maximum appeared tillers numbers, maximum appeared tiller numbers ($TilNo_{max}$), tiller number at final harvest ($TilNo_{FH}$) and tiller mortality plant^{-1} (= $TilNo_{max}$ - $TilNo_{FH}$) for three canaryseed, one spring wheat and one oat cultivar seeded on three dates in 2013 and 2014.

Cultivar	Stat.An.[1]	2013			Stat. An SEM	Sign.	2014			Stat. An. SEM	Sign.
		Early	Late	V.Late			Early	Late	V.Late		
		Thermal time from emergence to the onset of tiller appearance (°Cd)									
Togo		190a	193ab	201a	16.8	ns	196a	194a	194a	7.4	ns
Bastia		158a	200a	181a	20.5	ns	189a	207a	191a	20.0	ns
Keet		171a	161ab	190a	16.1	ns	201a	194a	212a	32.3	ns
Barrie		154a	108b	157a*	5.7	*	146a	206a	113ab*	16.9	+
Morrison		154a	123ab	150a	10.0	ns	177a	**148a**	**79b***	1.3	***
	SEM	16.6	15.6	12.1			10.4	23.8	19.8		
	Sign.	ns	*	+			+	ns	*		
		Tt from Em to the time when $TilNo_{max}$ plant^{-1} was reached (°C d)									
Togo		762ab	846ab	895b	31.5	ns	780ab	1047ab	912ab	61.6	ns
Bastia		789a	824abc	870b	23.4	ns	815ab	901abc	830bc	26.3	ns
Keet		781a	898a	**1057a**	26.2	*	875a	1104a	1028a	76.2	ns
Barrie		597c	646bc	629c	25.0	ns	762ab	715bc	683c	46.4	ns
Morrison		645bc	616c	640c	30.8	ns	682b	681c	673c	87.5	ns
	SEM	25.0	35.4	20.0			23.5	93.8	52.0		
	Sign.	**	*	***			*	*	**		
		Maximum number of appeared tillers plant^{-1}									
Togo		4.2a	3.3b	4.8a	0.51	ns	3.2a	3.5a	4.5a	0.4	ns
Bastia		3.4ab	3.8b	3.9ab	0.39	ns	3.1ab	3.6a	4.1a	0.25	+
Keet		3.4ab	4.6a	4.5a	0.38	ns	3.8a	3.8a	4.5a	0.18	ns
Barrie		3.3ab	3.4b	3.5ab	0.04	ns	3.4a	3.3a	3.9a	0.15	+
Morrison		1.7b	1.8c	2.0b	0.19	ns	1.9b	1.5b	2.2b*****	0.05	*
	SEM	0.50	0.13	0.29			0.29	0.19	0.21		
	Sign.	*	***	*			*	**	**		
		Number of tillers plant^{-1} at final harvest									
Togo		2.6a	1.3ab	2.6a	0.46	ns	2.1a	1.6ab	**3.3a***	0.30	*
Bastia		1.9ab	1.4ab	2.1a	0.19	ns	2.2a	2.4a	3.2ab	0.16	+
Keet		1.7ab	2.1a	1.8ab	0.30	ns	1.3ab	1.4abc	2.6abc	0.20	+
Barrie		1.2bc	0.4bc	0.4b	0.16	+	1.0bc	1.0bc	1.2bc	0.30	ns
Morrison		0.5c	0.1c	0.2b	0.09	+	0.2c	0.4c	**0.7c**	0.10	*
	SEM	0.35	0.16	0.28			0.16	0.16	0.32		
	Sign.	**	**	**			**	**	*		
		Tiller mortality plant^{-1}									
Togo		1.6a	2.0a	**2.2ab**	0.06	*	1.1b	1.9ab	1.2ab	0.17	ns
Bastia		1.5a	2.4a	1.8b	0.30	ns	0.9b	1.3b	1.0b	0.20	ns
Keet		1.7a	**2.5a**	**2.7ab***	0.31	***	2.6a	2.4a	1.9ab	0.28	ns
Barrie		2.1a	2.9a	3.1a	0.19	+	2.4a	2.3a	2.7a	0.35	ns
Morrison		1.2a	1.7a	1.9b	0.10	+	1.7ab	1.1b	1.5ab	0.11	+
	SEM	0.25	0.22	0.17			0.27	0.15	0.27		
	Sign.	ns	+	*			**	**	*		

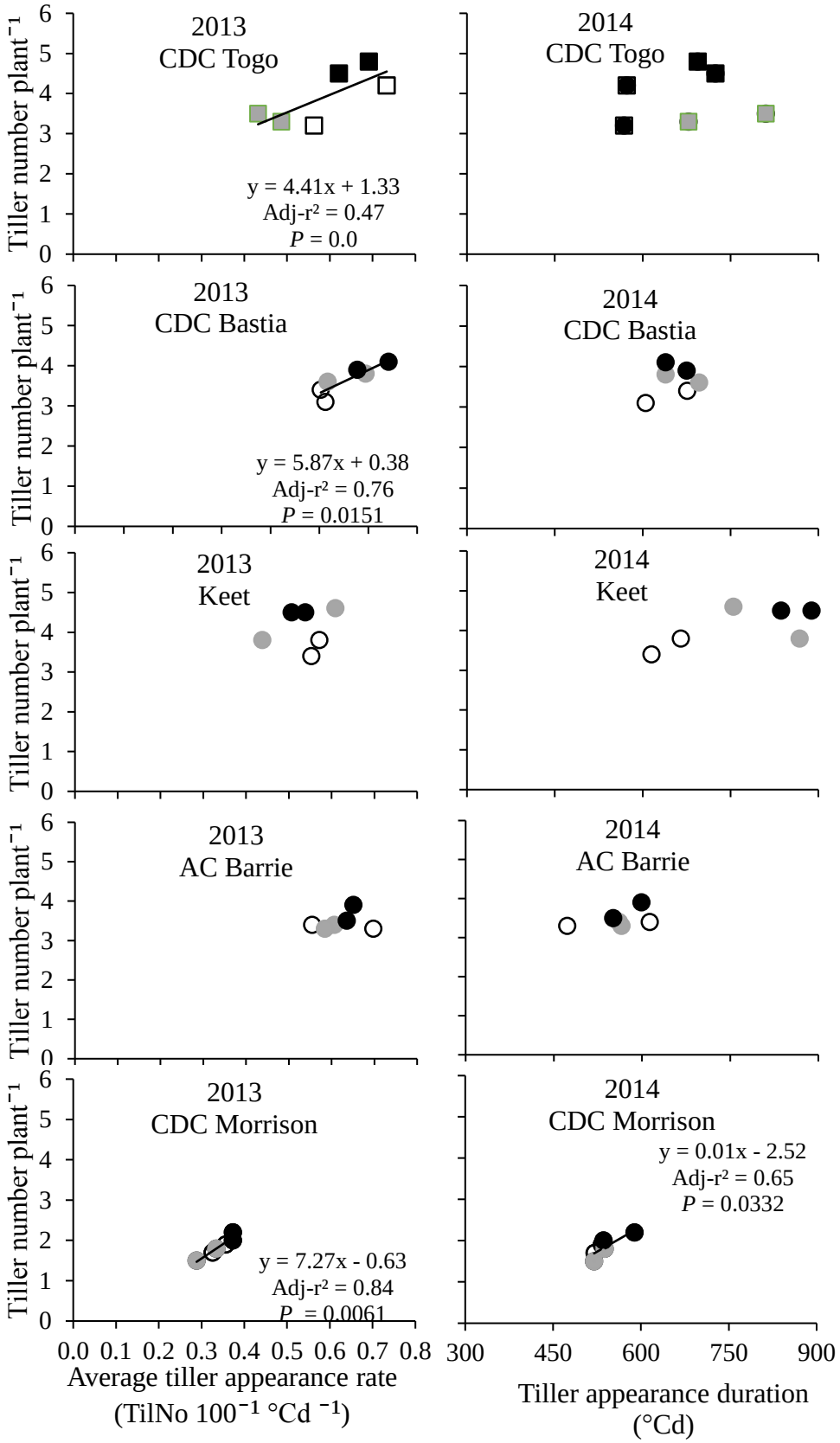
[1] Statistical analysis; [2] Standard Error of Mean; [3] Statistical significance; [4] Cultivar means within a response variable and within a year × seeding date combination followed by the same letters do not differ significantly at 5% level. Mean separations conducted by Tukey's tests; [5] Seeding date means in bold differ significantly from the early seeding date mean within a response variable and within a year × cultivar combination. Very late mean followed by an asterisk differ significantly from the late mean within a response variable and within a year × cultivar combination. Mean separations were conducted by Tukey's tests; [6]ns, +, *, ** and *** used to denote that the statistical significance within a response variable and within a year × seeding date and a year × cultivar combination is >0.1, ≤0.1, ≤0.05, ≤0.01 and ≤0.001. Mean values and their separation are based on pooled observations of six plants replication^{-1} and all four replications block^{-1}, thus only two blocks per year × cultivar combination have been used for the analysis.



A. 25. Tiller number plant^{-1} versus the modified Haun leaf stage (MHLS$_{YL}$) for three canaryseed, one wheat and one oat cultivar seeded early and late in 2013 and 2014. Mean values are derived from observations conducted on two blocks seeding date^{-1}, four replications block^{-1} and six plants replication^{-1}. For symbols and curves see figure legend. Symbols associated with data points indicate standard error.



A. 26. Tiller number plant^{-1} versus the thermal time after emergence (Tt) for three canaryseed, one wheat and one oat cultivar seeded early, late and very late in 2013 and 2014. Mean values are derived from observations conducted on two blocks seeding date^{-1}, four replications block^{-1} and six plants replication^{-1}. For symbols and curves see figure legend. Symbols associated with data points indicate standard error.

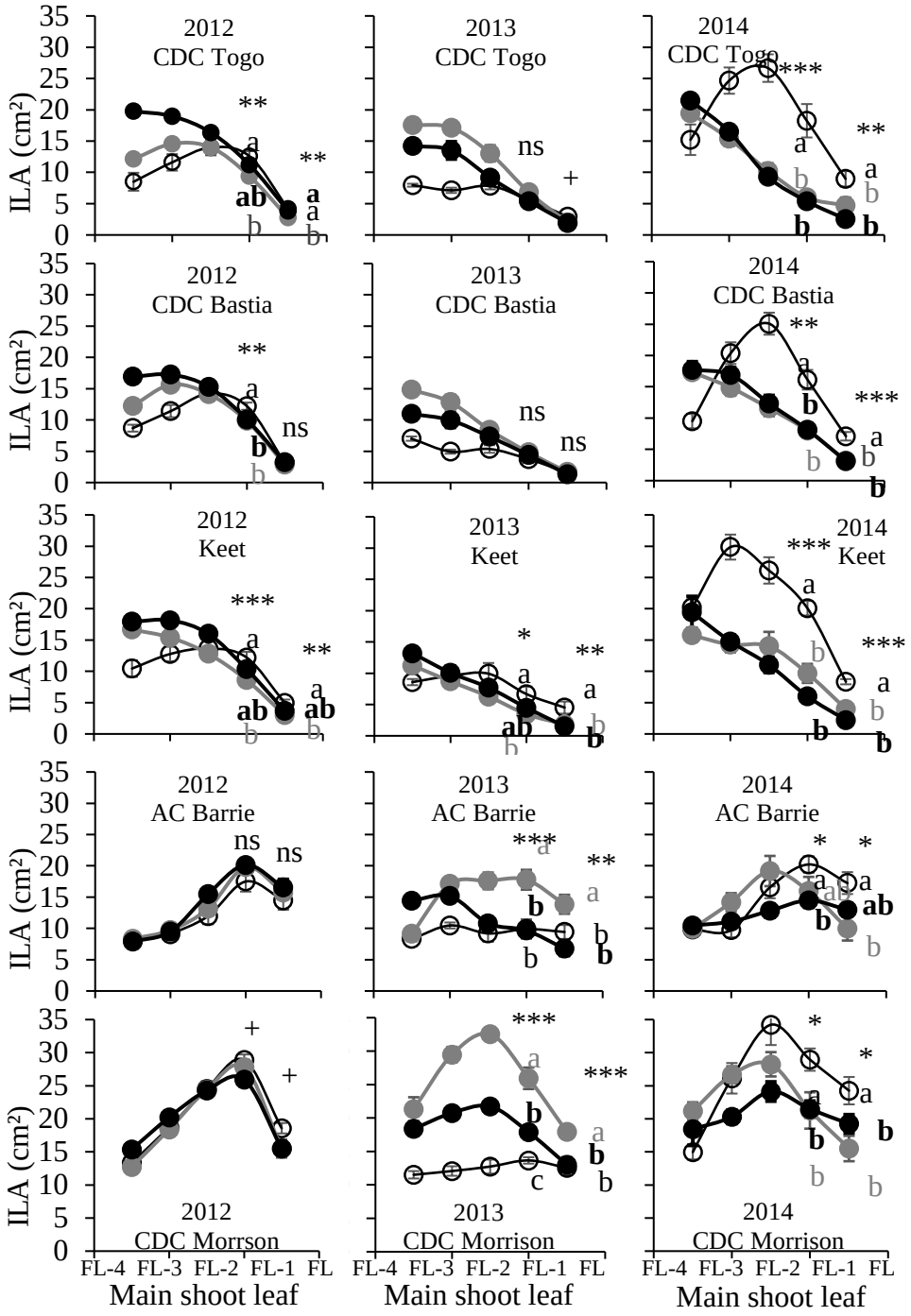


A. 27. Maximum tiller number plant $^{-1}$ versus average tiller appearance rate (left) and tiller appearance duration (right) for three canaryseed, one wheat and one oat cultivar seeded early, late and very late in 2013 and 2014. Mean values are derived from observations conducted on two blocks seeding date^{-1}, four replications block^{-1} and six plants replication^{-1}. For symbols and curves see figure legend. Symbols associated with data points indicate standard error.

A. 28. Mean percentage[1] of plants that produced the coleoptilar tiller (T0) and the main stem tillers (T1-T5) and the secondary tiller numbers produced plant^{-1} for three canaryseed, one spring wheat and one oat cultivar seeded on three dates in 2013 and 2014.

Tiller description	2013			2014		
	Early	Late	V.Late	Early	Late	V.Late
	CDC Togo					
T0	0.00	0.00	0.00	0.00	0.02	0.04
T1	0.77	0.58	0.42	0.69	0.27	0.67
T2	0.83	0.92	0.92	0.83	0.85	0.79
T3	0.71	0.79	0.88	0.75	0.60	0.83
T4	0.58	0.23	0.56	0.27	0.04	0.38
T5	0.40	0.06	0.27	0.08	0.02	0.17
Tsec/ plant	0.27	0.35	0.79	0.17	0.06	0.35
	CDC Bastia					
T0	0.00	0.00	0.00	0.02	0.00	0.00
T1	0.69	0.67	0.40	0.73	0.56	0.81
T2	0.56	0.90	0.77	0.85	0.83	0.90
T3	0.46	0.67	0.88	0.81	0.58	0.75
T4	0.67	0.31	0.46	0.23	0.27	0.40
T5	0.29	0.08	0.06	0.00	0.19	0.15
Tsec/ plant	0.00	0.58	0.38	0.06	0.23	0.56
	Keet					
T0	0.00	0.00	0.00	0.00	0.02	0.04
T1	0.67	0.81	0.27	0.63	0.52	0.67
T2	0.81	0.98	0.75	0.94	0.88	0.85
T3	0.67	0.90	0.83	0.77	0.69	0.85
T4	0.27	0.67	0.52	0.31	0.25	0.46
T5	0.17	0.21	0.13	0.06	0.02	0.17
Tsec/ plant	0.17	1.04	0.17	0.17	0.17	0.06
	AC Barrie					
T0	0.25	0.42	0.10	0.08	0.21	0.10
T1	0.94	0.90	0.69	0.69	0.83	0.98
T2	0.90	0.94	0.92	0.85	0.92	0.98
T3	0.56	0.29	0.88	0.67	0.71	0.75
T4	0.08	0.04	0.19	0.08	0.13	0.17
T5	0.00	0.00	0.02	0.02	0.00	0.00
Tsec/ plant	0.44	0.33	0.75	0.31	0.33	0.73
	CDC Morrison					
T0	0.08	0.21	0.08	0.00	0.06	0.02
T1	0.75	0.83	0.71	0.69	0.50	0.60
T2	0.48	0.54	0.85	0.67	0.38	0.73
T3	0.02	0.04	0.19	0.13	0.25	0.40
T4	0.00	0.00	0.00	0.00	0.00	0.04
T5	0.00	0.00	0.00	0.00	0.00	0.00
Tsec/ plant	0.00	0.02	0.02	0.02	0.08	0.04

[1] Percentages are derived from pooled observations on two blocks seeding date^{-1}, four replications block^{-1} and six tagged plants replication^{-1} by the plant destructive method.

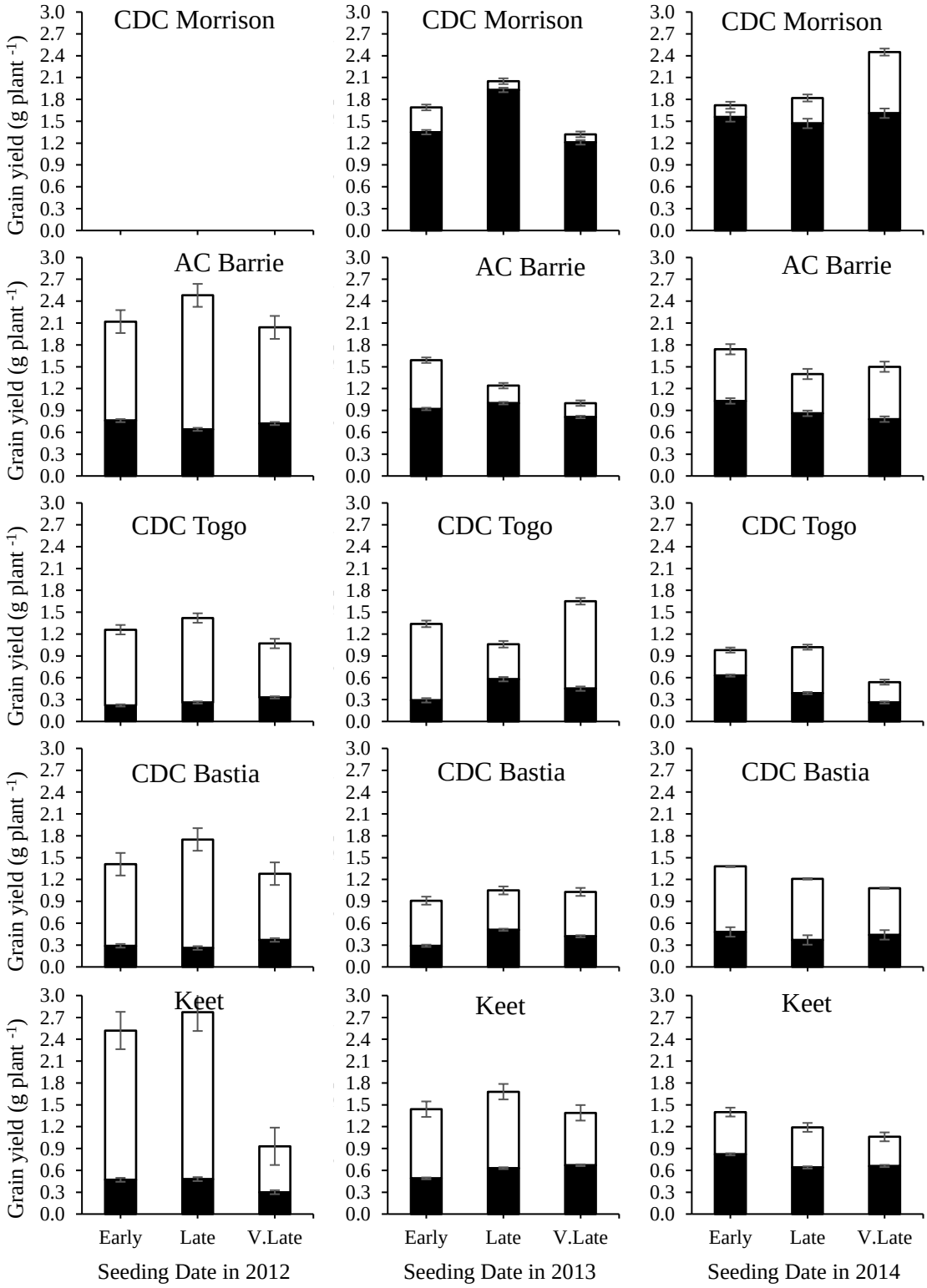


A. 29. Individual Leaf Area (ILA) (cm²) of the top five main stem phytomers for three canaryseed cultivars, one spring wheat and one oat cultivar, seeded early (open symbols-thin black line), late (grey closed symbols-grey line) and very late (black closed symbols-black line) in 2012 (left panels), 2013 (middle panels) and 2014 (right panels). Vertical bars, represent standard error when larger than symbols. Statistical analyses by year and cultivar were conducted for the penultimate and flag leaf only. Statistical analyses by year and cultivar were conducted for the penultimate and flag leaf only. ns, +, *, ** and *** used to denote that the statistical significance within a year × cultivar combination is >0.1, <0.1, <0.05, <0.01 and <0.001.

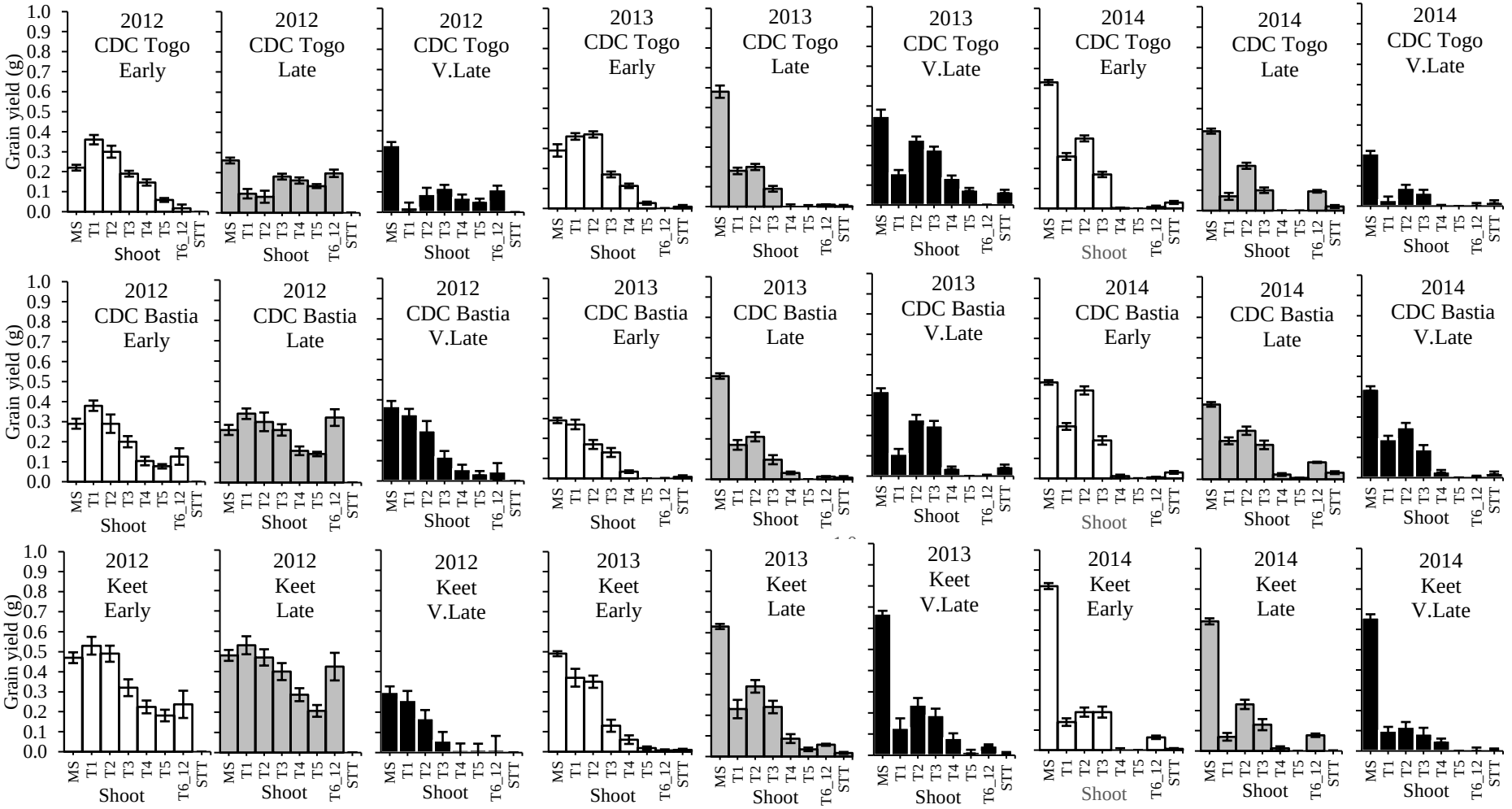
A. 30. Main stem and tillers grain yield of three canaryseed, one spring wheat and one oat cultivar seeded on three seeding dates in 2012, 2013 and 2014.

Cultivar	Stat. An.				Stat. An. SEM	Sign.				Stat. An. SEM	Sign.				Stat. An. SEM	Sign.
		2012					2013					2014				
		Early	Late	V.Late			Early	Late	V.Late			Early	Late	V.Late		
							Main stem grain yield (g)									
Togo		0.22c	0.26c	**0.33b**	0.029	*	0.29d	**0.58c**	**0.45d***	0.062	***	0.63cd	**0.39d**	**0.26d***	0.025	***
Bastia		0.29c	0.26c	0.37b	0.050	ns	0.29d	**0.51c**	**0.42d***	0.027	***	0.48d	**0.37d**	0.44cd	0.023	**
Keet		0.47b	0.48b	0.30b	0.054	+	0.49c	**0.63c**	**0.67c**	0.025	***	0.82c	**0.64c**	**0.66bc**	0.030	***
Barrie		0.76a	0.64a	0.72a	0.042	ns	0.92b	1.00b	**0.81b***	0.034	***	1.03b	0.86b	**0.78b**	0.076	*
Morrison		-	-	-	-	-	1.35a	**1.93a**	1.21a*	0.061	***	1.56a	1.47a	1.61a	0.130	ns
	SEM	0.065	0.039	0.048			0.025	0.043	0.031			0.079	0.054	0.060		
	Sign.	***	***	***			***	***	***			***	***	***		
							Tillers grain yield (g)									
Togo		1.04b	1.16b	0.74b	0.131	+	1.05a	**0.48b**	1.20a*	0.092	***	0.35a	**0.63ab**	**0.28c***	0.065	***
Bastia		1.12b	1.49ab	0.91ab	0.311	ns	0.62ab	0.54ab	0.61bc	0.109	ns	0.90a	0.84a	0.64abc	0.125	ns
Keet		2.05a	2.29a	**0.63b***	0.513	***	0.95a	1.05a	0.72ab	0.213	ns	0.58ab	0.55ab	0.40bc	0.122	ns
Barrie		1.36ab	1.84ab	1.32a	0.315	*	0.67ab	**0.24b**	**0.19cd***	0.075	***	0.71a	0.54ab	0.72ab	0.141	ns
Morrison		-	-	-	-	-	0.34b	**0.12b**	**0.11d**	0.079	*	0.16b	0.35b	**0.84a***	0.096	***
	SEM	0.396	0.461	0.145			0.187	0.130	0.134			0.111	0.110	0.155		
	Sign.	**	*	*			**	***	***			***	+	**		
							Whole plant grain yield (g)									
Togo		1.27b	1.42c	1.07b	0.140	ns	1.34ab	1.06bc	1.54a*	0.131	*	1.50a	**0.90b**	**0.49c***	0.079	***
Bastia		1.42b	1.75bc	1.28b	0.349	ns	0.92b	1.05c	1.16a	0.154	ns	1.37a	1.20b	1.06b	0.141	ns
Keet		2.55a	2.77a	**1.00b**	0.576	**	1.48a	1.66ab	1.38a	0.228	ns	1.40a	1.19b	1.02bc	0.132	ns
Barrie		2.33a	2.48ab	2.03a	0.396	ns	1.70a	**1.24bc**	**1.00a**	0.133	***	1.74a	1.40ab	1.50b	0.177	ns
Morrison		-	-	-	-	-	1.77a	2.00a	**1.33a**	0.157	**	1.71a	1.95a	**2.44a**	0.175	*
	SEM	0.500	0.492	0.177			0.219	0.148	0.165			0.146	0.151	0.164		
	Sign.	***	**	**			***	***	ns			ns	***	***		

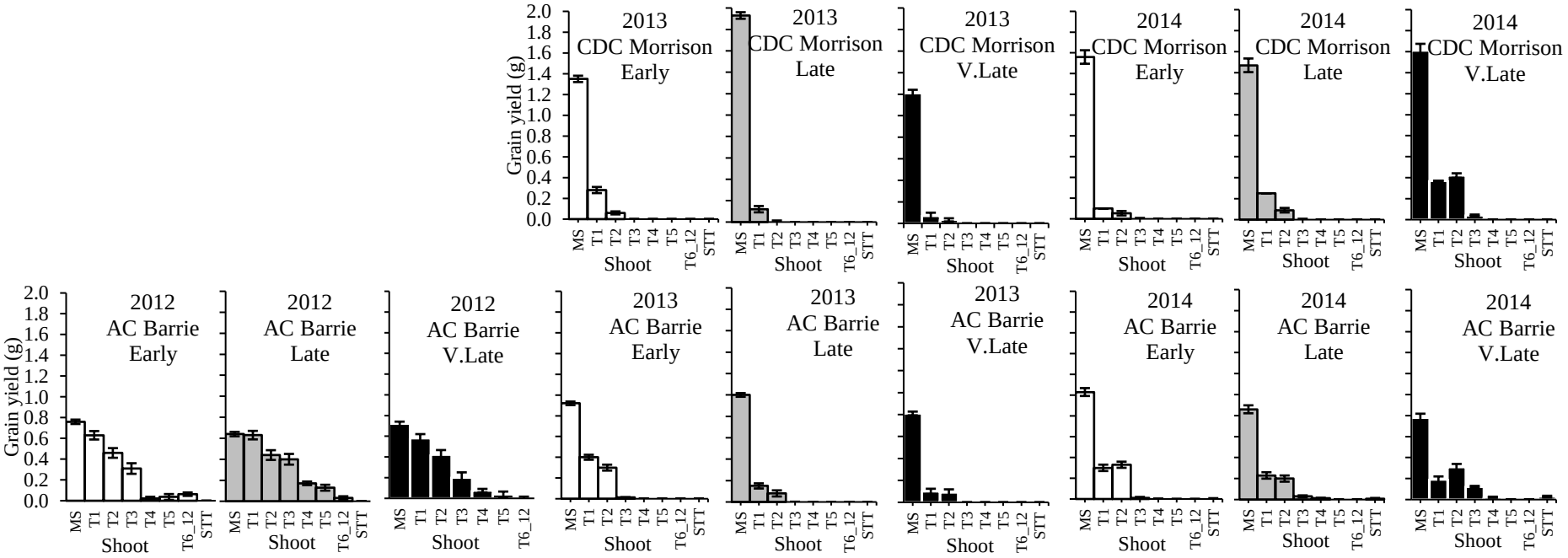
[1] Cultivar means within a Year×SD combination followed by the same letters do not differ significantly at 5% level. Means separation conducted with Tukey test.
[2] SD means within a Year×Cultivar combination in bold differ significantly from the means of early SD. V.Late means followed by an asterisk differ significantly from the Late means within a Year×Cultivar combination.
[3]ns, +, *, ** and *** used to denote that the statistical significance of the data within a column and a year×cultivar combination is >0.1, >0.05, >0.01, >0.001 and <0.001.



A. 31. Main stem (solid bars) and tiller (empty bars) grain yield (g plant $^{-1}$) for three canaryseed, one spring wheat and one oat cultivar seeded at three dates in 2012, 2013 and 2014. Bars on top of each column represent standard error.



A. 32. Main stem- (MS) and tiller- (T) derived grain yield for three canaryseed cultivars seeded early (empty bars), late (grey-closed bars) and very late (black-closed bars) in 2012, 2013 and 2014. The number accompanying the letter T denotes the leaf on MS from the sheath of which the tiller grew. The abbreviation T_{6_12} is used for the sum of the grain yield derived from T6 to T12. STT abbreviation is used for the sum of the grain yield derived from the secondary, tertiary and higher-ranked tillers.



A. 33. Main stem- (MS) and tiller- (T) derived grain yield for a spring wheat and an oat cultivar seeded early (empty bars), late (grey-closed bars) and very late (black-closed bars) in 2012, 2013 and 2014.The number accompanying the letter T denotes the leaf on MS from the sheath of which the tiller grew. T_{6_12} STT abbreviation is used for the grain yield derived from the T6 to T12. STT abbreviation is used for the grain yield derived from the secondary, tertiary or higher-order tillers.